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SHEET WEBS OF LINYPHIROID SPIDERS (ARANEAE: LINYPHIIDAE, PIMOIDAE): THE LIGHT OF DIVERSITY HIDDEN UNDER A LINGUISTIC BASKET

GUSTAVO HORMIGA^{1,2} AND WILLIAM G. EBERHARD^{3,4}

ABSTRACT. Photographs of the webs of approximately 113 species in 52 genera show that the web architecture of linyphioid spiders (Linyphiidae and Pimoidae) present many variations on a single basic pattern. Nearly all species built webs with a more or less horizontal, continuous sheet with an open space just below the sheet. However, the details in the designs showed great diversity; we recognized >50 web traits, including positions relative to the ground or large objects; sheet shapes and orientations; secondary sheets; “slime” on the sheet; patterns and densities of lines in sheets; visible droplets on sticky lines; upward and downward directed dimples in the sheet with tensor lines; primary and secondary frame lines; retreats; and the presence, location, and designs of associated tangles. This survey probably substantially underestimates both intraspecific and intrageneric diversity of web forms. Intrageneric comparisons in just over 20 genera documented varying degrees of intrageneric variation; some genera show striking differences. Several web designs were widely distributed: sheets with dense tangles above commonly had arrays of lines attached to the sheet’s upper surface; downward dimples in sheets commonly occurred at sites where the sheet curved upward, but upward-directed dimples were rare and small; and sheets built next to the surface of the ground almost always lacked extensive tangles above them. New web patterns not previously reported for linyphiid webs include: sandwich webs (pairs of closely spaced, otherwise naked sheets); extensive vertical sheets next to tree trunks; tubular retreats at the edges of the

sheet where the spider rests; trough-like sheets just above the upper surface of a curled leaf; sizeable, apparently sticky droplets densely covering many lines that were apparently placed in pairs in the sheet; long sheet lines that converge at one corner; runways to a sheltered site where the spider waits beyond the sheet’s edge; and apparent skeleton lines in the sheet (probably from early stages of construction). Patterns of lines within the sheet may reflect patterns of movement during sheet construction behavior. We propose that some webs on the substrate function to extend the spider’s sensory field rather than detain prey and that some tangles below and perhaps some above the sheet may function to defend the spider from enemies. A suite of linyphiid traits, including leg, chelicera, and spinneret morphology; details of web design, such as numerous small upward-directed dimples in dome-shaped sheets but fewer, large downward-directed dimples in cup-shaped sheets; and attack behavior, appears to function to increase the speed with which spiders attack prey. The functions of many architectural features remain obscure.

INTRODUCTION

Current understanding of spider phylogeny indicates that orb webs are ancient and evolved more than 165 Mya in the late Triassic or Early Jurassic; several large extant families subsequently abandoned orbs, either to build other types of webs or to forage without webs (Garrison et al., 2016; Dimitrov et al., 2017; Fernández et al., 2018a,b; Coddington et al., 2019; Kallal et al., 2021; Kulkarni et al., 2021). One group that may have abandoned orbs to build other designs is the large araneoid family Theridiidae (but see Kallal et al., 2021; Kulkarni et al., 2021), which has

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rightly been considered the “queen of web diversity,” with its gumfoot webs, sheets, “rectangular orbs,” star webs, single-line webs, and so on (Eberhard et al., 2008). Another monophyletic web-building araneoid group, the linyphioids (Linyphiidae and Pimoidae), is an even larger web-building lineage descended from orb weavers (Arnedo et al., 2009; Dimitrov et al., 2017; Wheeler et al., 2017). The sister group of linyphioids may be the small sheet-weaving family Cyatholipidae (Kallal et al., 2021; Kulkarni et al., 2021).

Linyphioids constitute a dramatic evolutionary success in two senses: they include more than 4,800 named species (about 10% of all spider species) (World Spider Catalog, 2022), with many more yet to be described (e.g., Platnick and Raven, 2013), and they are common in some areas and they are numerically dominant family in some temperate areas (Bradley, 2013; Bristowe, 1941; Wheeler, 1973; Alderweireldt, 1994). Nevertheless, despite being unusual among spiders, in that they are especially diverse in temperate areas where they have been the subjects of extensive ecological studies (Turnbull, 1960; Toft, 1980, 1987, 1989; Suter, 1981; Nentwig, 1983; Nentwig and Heimer, 1983; Alderweireldt, 1994; Rybak, 2007; Bednarski et al., 2009; Peterson et al., 2010), knowledge of their web building behavior is limited to only a few studies (Emerton, 1902; Benjamin and Zschokke, 2004; Eberhard, 2020). The construction behavior of two species of *Linyphia* Latreille, 1804, was characterized as lacking regular patterns and consisting of only two types of nonstereotyped behavior, one of which was “surprisingly simple” (Benjamin and Zschokke, 2004: 125).

Linyphioids have been characterized as poor cousins to theridiids for building only a single web design—horizontal sheet webs (Emerton, 1902; Nielsen, 1932; Kaston, 1948; Bristowe, 1958; Buche, 1966; Comstock, 1967; Benjamin et al., 2002; Benjamin and Zschokke, 2004). Alternatively,

seen from the perspective of their great evolutionary success, this sheet web design has been extraordinarily successful over evolutionary time. Several more or less minor design differences in linyphiid webs were listed in summaries by Nielsen (1932), Bristowe (1941), and Shinkai (1979): concave or cup-shaped sheets (in *Frontinellina frutetorum* (C. L. Koch, 1835)); convex or domed sheets (in *Neriere radiata* (Walckenaer, 1841)); webs with retreats at the edge (*Neriere montana* (Clerck, 1757)), *Labulla thoracica* (Wider, 1834), *Lepthyphantes minutus* (Blackwall, 1833), and *Erigone* Audouin, 1826); the addition of “slime” to the sheet in *Tapinopa* Westring, 1851, spp.; webs sited on or near the substrate; webs on and around vegetation; webs spanning large open spaces; and methods of anchoring sheets that include a hammocklike arrangement utilizing only lines at the edges of the sheet in *Stemonyphantes lineatus* (Linnaeus, 1758), *Floronia bucculenta* (Clerck, 1757), *Labulla thoracica*, *Tenuiphantes tenuis* (Blackwall, 1852), and *Agyneta* (= *Meioneta*) *rurestris* (C. L. Koch, 1836), supporting lines that extend upward in *L. minutus*, downward in a few species of *Linyphia*, and run both upward and downward in other *Linyphia*. Another variation is in the shape of the sheet: those of *Floronia bucculenta* and *Tenuiphantes tenuis* are more or less flat and horizontal; that of *Labulla thoracica* is flat but slanted from a crevice where the spider is concealed; the sheet of *Linyphia triangularis* (Clerck, 1757) is slightly domed; that of *Neriere radiata* is more steeply domed; and those of *Neriere montana* and *Neriere clathrata* (Sundevall, 1830) are cup- or hammock-shaped, with a number of small depressions where anchor lines pull the sheet downward. Other variants that have been described include saddle-shaped sheets in *Linyphia triangularis* (Herberstein, 1997), reductions of the sheet in *Drapetisca socialis* (Sundevall, 1833) (Kullmann, 1961; Schütt, 1995), and complete

loss of webs in species living in ant nests (Bristowe, 1958; Cushing, 2012). In *Bathypantes eumenis* (L. Koch, 1879), some webs are very sparse meshes of lines just above, near the substrate, and spiders attack passing prey directly (Rybák, 2007).

Linyphioid webs are often said to lack sticky lines, but microscopic examinations have revealed droplet-bearing lines in the sheets of species in at least seven genera (Wiehle, 1956; Millidge, 1988; Peters and Kooor, 1991; Benjamin and Zschokke, 2002; Eberhard, 2021); in some species the large majority of lines in the sheet bore droplets. Sticky lines also occur in webs of mature males. Don Buckle (in a letter to G. H., June 1994) also reported the presence of sticky silk in the webs of adult males of the erigonines *Diplocephalus cuneatus* (Emerton, 1909); *Erigone atra* Blackwall, 1833; *Soucron arenarium* (Emerton, 1925); *Collinsia plumosa* (Emerton, 1882); and *Pelecopsis moesta* (Banks, 1892), and of the “micronetine” *Centromerus sylvaticus* (Blackwall, 1841) and in *Agyneta* Hull, 1911, sp. Sticky silk production by adult males also has been reported in the erigonine *Masoncus pogonophilus* Cushing, 1995 (Cushing, 1995). Simple tests demonstrated that the droplet-bearing lines of several genera adhered to smooth objects (Millidge, 1988; Eberhard, 2021). These droplets apparently self-assemble during and following web construction, probably reinforcing adhesions between lines and perhaps also prey (Eberhard, 2021). Nevertheless, prey that strike linyphiid webs are retained only very briefly if the spider does not attack (Nielsen, 1932; Turnbull, 1960).

Linyphioid Systematics and Phylogeny

The linyphioid clade comprise the families Pimoidae and Linyphiidae, both members of the Araneoidea, the ecribellate orb weavers (Griswold et al., 1998; Hormiga and Griswold, 2014). The typical orb web architecture consists of a frame holding radii

that support a spiral adhesive thread. Although some of the most emblematic araneoids build orb webs, such as the majority of Araneidae and Tetragnathidae, other araneoid groups build distinctly different webs, such as the cobwebs of theridiids or the sheet webs of linyphiids, or have abandoned foraging webs altogether, such as the pirate spiders (Mimetidae). With close to five thousand described species, linyphiids are the most species-rich lineage of Araneoidea. The vast majority of those species are members of the Linyphiidae (over 4,700 species in 625 genera), the second largest spider family (World Spider Catalog, 2022). Pimoids comprise only two genera and 85 species (all but one in the genus *Pimoa*). The monophyly of linyphiids is supported by five synapomorphies: cheliceral stridulatory striae; patella-tibia autospasy; an enlargement of the peripheral cylindrical spigot base on the posterior lateral spinnerets; a 9+0 axonemal pattern in the sperm; and an ectal cymbial process in the male palp (Wunderlich, 1986; Hormiga, 1993, 1994a,b; Michalik and Hormiga, 2010; Hormiga et al., 2021). The monophyly of Pimoidae is supported by four synapomorphies: a modified macroseta on a dorsoectal cymbial process; a retrolateral cymbial sclerite (pimoid cymbial sclerite); an alveolar sclerite; and the absence of aciniform silk gland spigots on the female posterior median and lateral spinnerets (Hormiga, 1994b; Hormiga et al., 2005, 2021). Linyphiid synapomorphies include several genital traits: an intersegmental paracymbium, supratégulum, a distal supratégular apophysis, and a column and radix (Hormiga et al., 2021). The phylogenetic structure of the Linyphiidae tree is for the most part poorly understood.

In contrast with most araneoid families (e.g., Theridiidae or Araneidae), the somatic morphology of linyphiids is rather conservative (Fig. 1), except for the prosomal modifications (lobes, sulci and pits, setae, etc.) of many erigonine males (Hormiga,

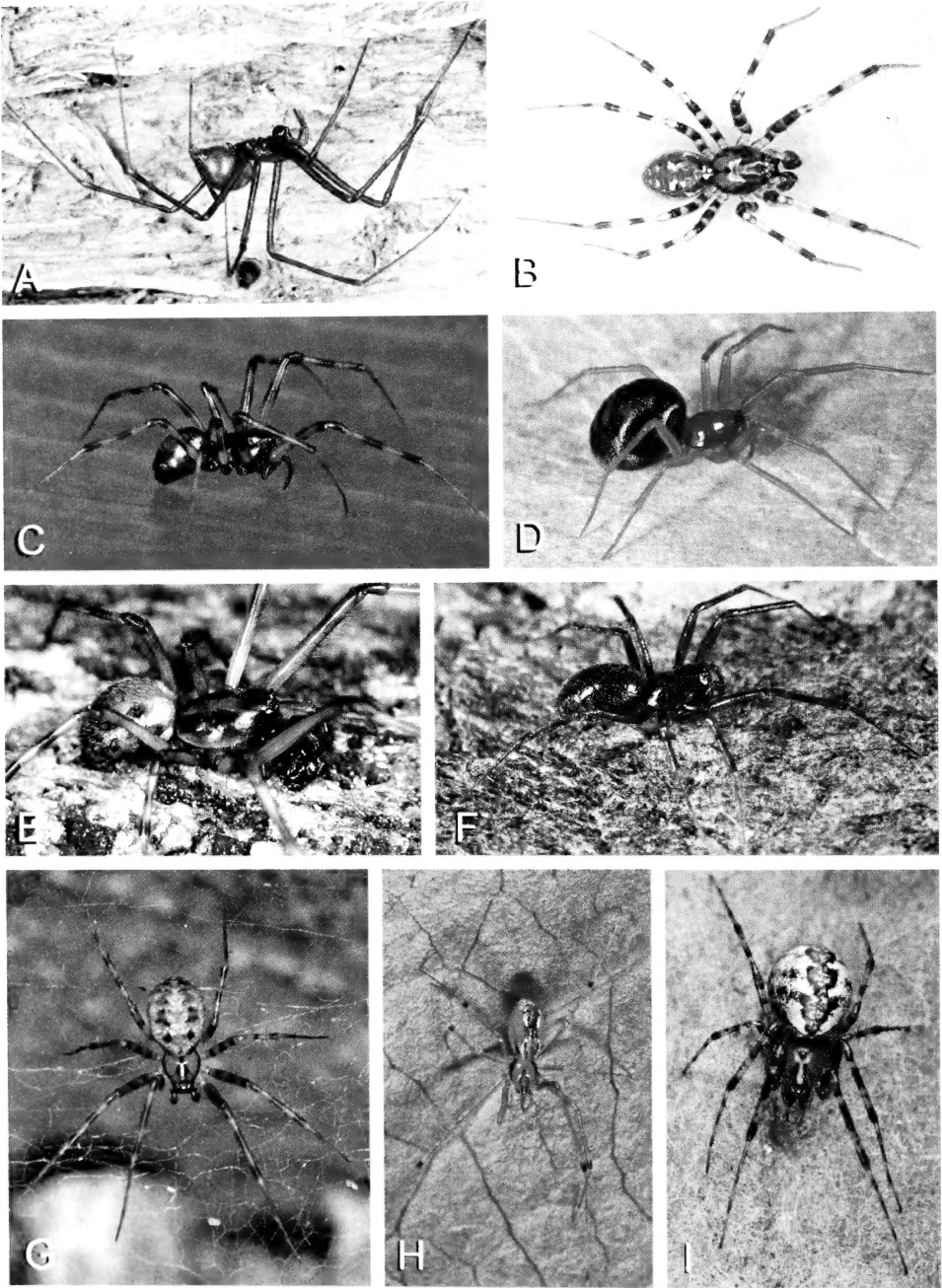


Figure 1. Habitus images of linyphioid spiders. (A) Pimoidae and (B–I) Linyphiidae habitus photographs. (A) *Pimosa cthulhu* Hormiga, 1994, female from California (DSC_5065). (B) *Putaoa seediq* Hormiga & Dimitrov, 2017 (Stemonyphantinae), male from Taiwan. (C) *Dubiaranea* sp. (MPME clade), female from Ecuador. (D) *Laminacauda rubens* Millidge, 1991 (Erigoninae), female from Juan Fernandez Islands (DSC_1027). (E) *Orsonwelles malus* Hormiga, 2002, male from Kauai. (F) *Novafroneta* sp. (Mynogleninae), female from New Zealand (DSC_2505). (G) *Labulla thoracica* (Wider, 1834), female from Zealand, Denmark. (H) *Laetesia raveni* Hormiga & Scharff, 2014, female from New South Wales, Australia (DSC_2950). (I) *Ptychoyphantes costatus* (Hentz, 1850), female from Maryland.

2000), which are probably evolving under sexual selection (Michalik and Uhl, 2011; Lin et al., 2021). The paucity of variation in the somatic characters of linyphiids contrasts with the remarkable diversity of their genitalic structures, which are probably also under sexual selection (Eberhard, 1985). We argue below that several aspects of this linyphioid conservatism in morphology, in particular their relatively long thin legs, their moderately robust chelicerae with teeth on both margins of the basal segment (Draney and Buckle, 2017; Wolff et al., 2022), their moderately long cheliceral fangs (*Pimoa* is an exception) (Wolff et al., 2022), and their reduced number of aciniform silk gland spigots may be associated with their web architecture, which facilitate rapid attacks but are unable to retain prey for long periods because of their relatively limited adhesion to prey. Attacks on prey were very rapid in *Linyphia triangularis* and *Microlinyphia pusilla* (Sundevall, 1830) (Bristowe, 1941; Benjamin et al., 2002). In recordings (at 30 frames/s) of 12 attacks by *Neriene coosa* (Gertsch, 1951) on live *Drosophila* prey that were dropped onto the sheet a median of 13.5 body lengths from the spider, the spider delayed only a median of 0.03 s before first responding and ran toward the prey at a median speed of 57 body lengths/s; spiders reached the prey in a median of 0.37 s (minimum 0.17 s) (Eberhard, 2021, unpublished data).

The first quantitative cladistic analyses of linyphiids were based on small taxonomic samples but offered explicit phylogenies based on some of the main morphological features of the subfamilies, including spinneret spigot morphology (Hormiga, 1994a,b). Subsequent cladistic work focused primarily on Erigoninae, the largest linyphiid subfamily (e.g., Hormiga, 2000; Miller and Hormiga, 2004; Frick et al., 2010; Tu and Hormiga, 2011); Mynogleninae (Frick and Scharff, 2014); and newly described pimoid genera (later transferred to stemonyphantine Linyphiidae) (Hormiga, 2003;

Hormiga et al., 2005; Hormiga and Tu, 2008). Arnedo et al. (2009) carried out the first linyphiid analysis that used multigene nucleotide sequence data (from the mitochondrial markers cytochrome *c* oxidase subunit I and 16S and the nuclear markers 28S, 18S, and histone H3), combined with morphological data. Their character matrix included 35 linyphiids representing the subfamilies Stemonyphantinae, Mynogleninae, Erigoninae, and Linyphiinae and 12 species representing nine other araneoid families. Their analyses supported the monophyly of linyphioids, Pimoidae, Linyphiidae, Erigoninae, and Mynogleninae and indicated that the stemonyphantines are the lineage sister to all other Linyphiidae. The Micronetinae (a large group with many northern hemisphere species that includes the genera *Microneta*, *Agyneta*, and *Lepthyphantes*) was shown to be paraphyletic with respect to Erigoninae.

Subsequent molecular work that used the same genes but with a much larger taxon sample (Dimitrov et al. 2012, 2017; Wang et al., 2015; Tian et al., 2022) has corroborated many of those groups but also suggested a much more complex picture of the phylogeny of Linyphiidae. All more recent analyses have confirmed the hypothesis of Arnedo et al. (2009) that micronetines are paraphyletic. The Mynogleninae, a southern hemisphere group with a disjunct distribution pattern (tropical Africa, New Zealand, and Australia), have been consistently found to be monophyletic in both morphological (Hormiga, 1994b; Frick and Scharff, 2014) and molecular analyses (Arnedo et al., 2009; Dimitrov et al., 2012; Wang et al., 2015). More recent morphological cladistic analyses have helped delimit poorly studied groups, such as the mounded posterior median eyes (MPME) clade and the *Pocobletus* clade (Silva-Moreira and Hormiga, 2021), but the broad picture of the linyphiid tree remains poorly defined. Hormiga et al. (2021) recently addressed the family limits of both Pimoi-

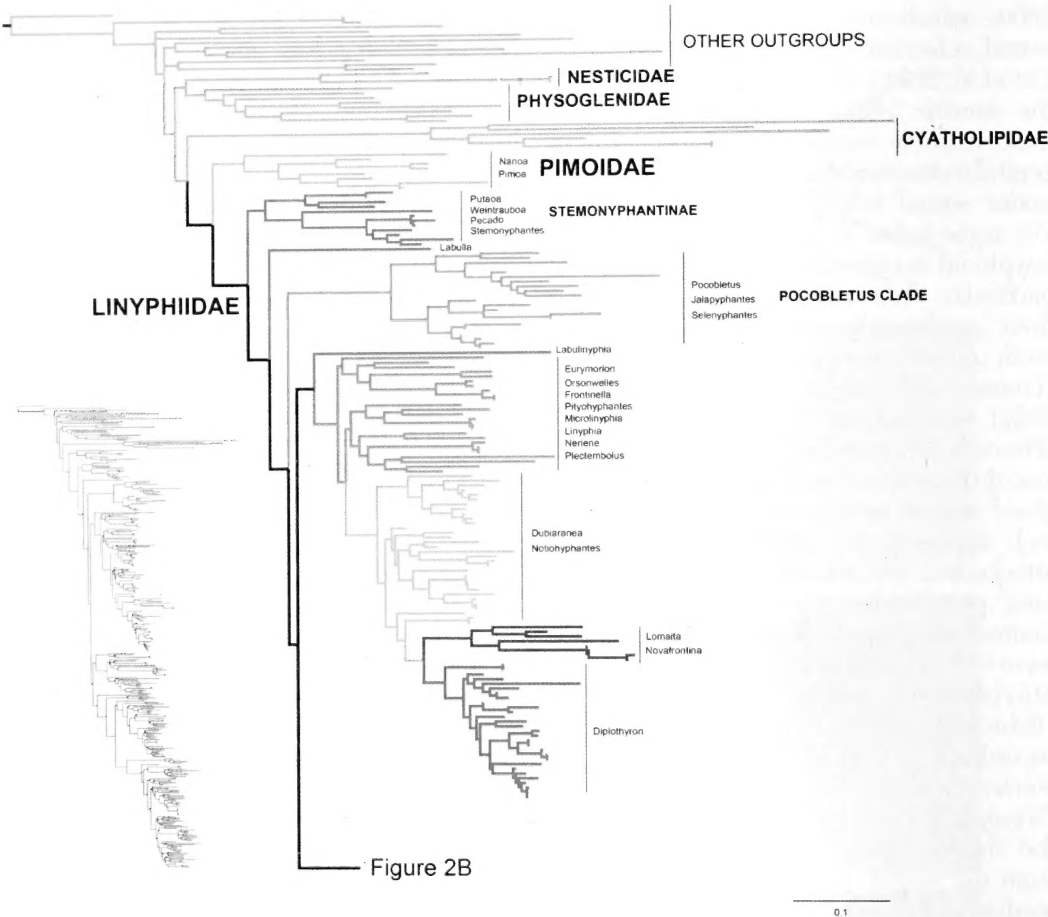


Figure 2. Phylogenetic tree of linyphioids. Phylogenetic relationships of linyphioids. This cladogram is a simplified version of the optimal maximum likelihood tree resulting from a combined analysis of morphological and molecular data (cytochrome *c* oxidase subunit I, 16S, 18S, and histone H3) of Silva-Moreira, Kulkarni and Hormiga (in prep). The genera represented in the various clades and grades are listed on the right.

dae and Linyphiidae with Sanger sequences and recircumscribed the former to only include *Pimoida* and *Nanoa*. The genera *Weintrauboa* and *Putaoa* (formerly in Pimoidae) and *Pecado* were placed in an expanded linyphiid subfamily, Stemonyphantinae, the sister lineage of a clade that includes all other linyphiids. The most comprehensive hypothesis regarding the higher level phylogeny of linyphioids (Silva-Moreira et al., in preparation), on the basis of combined morphological and target sequencing data, is summarized in Figure 2.

To summarize our current knowledge of linyphioid phylogeny, the monophyly of linyphioids Pimoidae and Linyphiidae is well supported. The subfamilies Stemonyphantinae, Mynogleninae, and Erigoninae also appear to be monophyletic, but all other subfamilial groups (Linyphiinae, Micronetinae, Dubiaraneinae, and Ipainae; see Tanasevitch, 2022) are not. What are the closest relatives of linyphioids? The answer to this question can help elucidate the origin of linyphioid sheet webs. The difficulties of resolving this



Figure 2. Continued.

problem derive from the challenges of addressing the more inclusive and recalcitrant question of the phylogenetic relationships of the araneoid families. An early cladogram based on morphological and behavioral characters (Griswold et al., 1998) suggested that linyphioids were the sister group of a lineage that included theridiids, nesticids, synotaxids, and cyatholipids, but this hypothesis has not been supported by any subsequent molecular phylogenetic analysis. Target gene analyses with Sanger sequencing data have resulted in multiple incongruent araneoid topologies (e.g., Blackledge et al., 2009; Dimitrov et al., 2012, 2017; Wheeler et al., 2017) and different linyphioid sister groups. High throughput sequencing methods subsequently offered still different answers on

the basis of hundreds of markers, first with the use of transcriptomic data (e.g., the analysis of Kallal et al. (2021), which included representatives of all araneoid families) followed by analyses of ultraconserved elements (UCEs; Kulkarni et al., 2021). The results of these transcriptomic analyses were not congruent, however, with those of the UCE data; and paradoxically, the incongruent placements of groups were strongly supported in both hypotheses. Both transcriptomes and UCEs place theridiids as the sister group of a lineage that includes all other araneoid families, but they disagree on the sister group of linyphioids. Transcriptomes suggest that linyphioids are sister to a lineage that includes cyatholipids and synaphrids (Kallal et al., 2021: fig. 3). UCEs place linyphiids and pimoids in a clade along

with cyatholipids, physoglenids, and nestioids (Kulkarni et al., 2021: fig. 1), but with cyatholipids nested between pimoids and linyphiids. Both hypotheses place linyphiids and pimoids in a lineage with sheet and irregular web builders. The aforementioned synapomorphies of linyphioids suggest that the placement of cyatholipids between pimoids and linyphiids might be incorrect. Figure 2 provides a summary of the most recent phylogenetic hypothesis of linyphioid relationships from morphological and DNA sequence data. Considering the phylogeny in Figure 2, the similarities between the webs of cyatholipids and some physoglenids (Dimitrov et al., 2017; see also Figs. 3–10) compared with linyphioid webs, it appears that the common ancestor of these three groups probably built sheet webs of some sort.

The Spinneret and Spigot Morphology of Linyphioids

One of the defining synapomorphies of Araneoidea is the presence of a triplet (or triad) of silk gland spigots in the posterior lateral spinnerets. The araneoid triad comprises two spigots that are connected to the aggregate silk glands and one that is fed by the flagelliform gland. The former glands produce the gluey, viscose material of the sticky silk threads, and the latter produces the axial fibers (Kovoor, 1977; Coddington, 1989). In general, this triad is present in all araneoids regardless of their web architecture (Griswold et al., 1998; Hormiga and Griswold, 2014) but is reduced or absent (presumably lost) in lineages that have abandoned foraging webs (e.g., malkarids, mimetids, the anapid *Holarchaea*). In adult araneoid males the triad is usually reduced to nonfunctional nubbins; erigonine linyphiids and cyatholipids offer an exception to this pattern: the adult males retain the araneoid triad (Hormiga, 2000; Griswold, 2001; Hormiga and Griswold, 2014).

Despite the enormous species diversity of the linyphioid lineage, their spinning fields share common morphological patterns. Early scanning electron microscopy studies of the linyphiid spinnerets go back to the works of Coddington (1989) for *Frontinella pyramitela* (Walckenaer, 1841) and Peters and Kovoor (1991) for *Linyphia triangularis*. Hormiga (1994a,b) followed with a survey of the spigot morphology in *Pimoida* (nine species) and in Linyphiidae (nine species in nine genera). Schütt (1995) studied spigot morphology of *Drapetisca socialis*. The studies of Hormiga and Miller (Hormiga, 2000; Miller and Hormiga, 2004; Miller, 2007) expanded the sample of erigonines. Hormiga (2002) surveyed the spigot morphology of 10 of the 13 known species of the Hawaiian genus *Orsonwelles*. Linyphioids exhibit the typical araneoid spigot morphology (Hormiga, 1994b; Griswold et al., 1998), except for the relatively small number of aciniform spigots in the posterior median spinnerets and posterior lateral spinnerets, a condition taken to an extreme in some species of *Pimoida*; *Nanoa enana* Hormiga, Buckle, & Scharff, 2005; and *Stemonyphantes*, in which adults lack aciniform spigots entirely (Hormiga, 1994a,b; Hormiga et al., 2005). This reduction is probably associated with a failure to attack prey by wrapping them in silk and reduced prey wrapping in general (Eberhard, 1967). Another feature of the linyphioid spinning fields is the enlargement of the base of the peripheral cylindrical gland spigot on the posterior lateral spinnerets relative to the sizes of other cylindrical spigots (a synapomorphy of this lineage).

Linyphioids have the araneoid triad responsible for spinning sticky silk, with a few exceptions (e.g., *Drapetisca socialis* has only the flagelliform spigot; Schütt, 1995). As in most araneoids, the triad is “lost” after the last molt in males. The triad is usually present in the adult males of Erigoninae; in the mynoglennines *Haplinis diloris* (Urquhart, 1886) and *Novafroneta vulgaris* Blest,

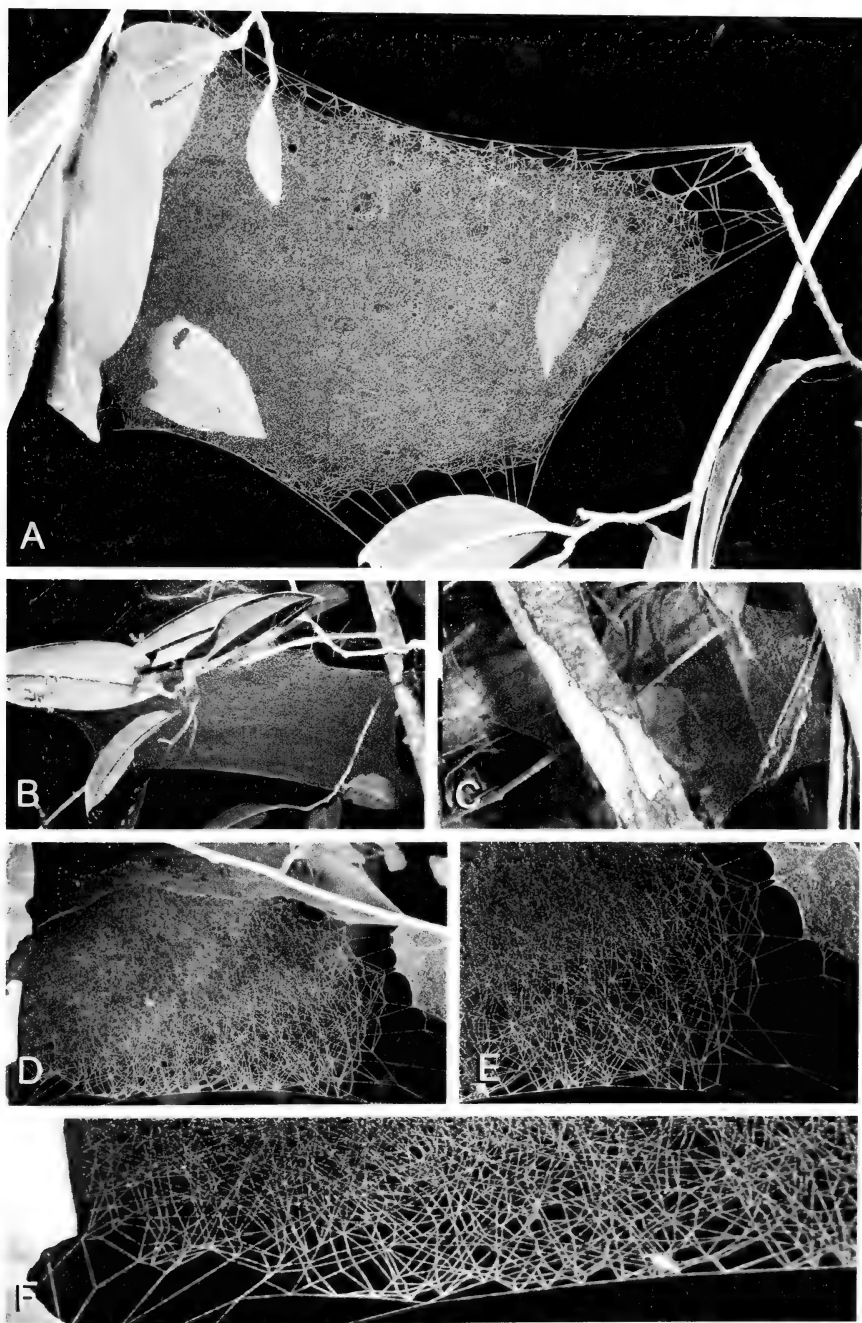


Figure 3. Cyatholipidae webs (1). (A) *Forstera* sp., female. Australia, Queensland, Atherton Tablelands (DSC_8144.NEF). (B) *Forstera* sp., female. Australia, Queensland, Atherton Tablelands (DSC_8129.NEF). (C) *Matilda* sp., female. Western Australia, Walpole-Nornalup National Park (DSC_0218.NEF). (D–F) *Forstera* sp., female. Australia, Queensland, Atherton Tablelands, Danbulla State Forest (GH020421_R08_32_AUS.TIF, GH020421_R08_35_AUS.TIF, Forstera_GH020421_R08_37_AUS.TIF).

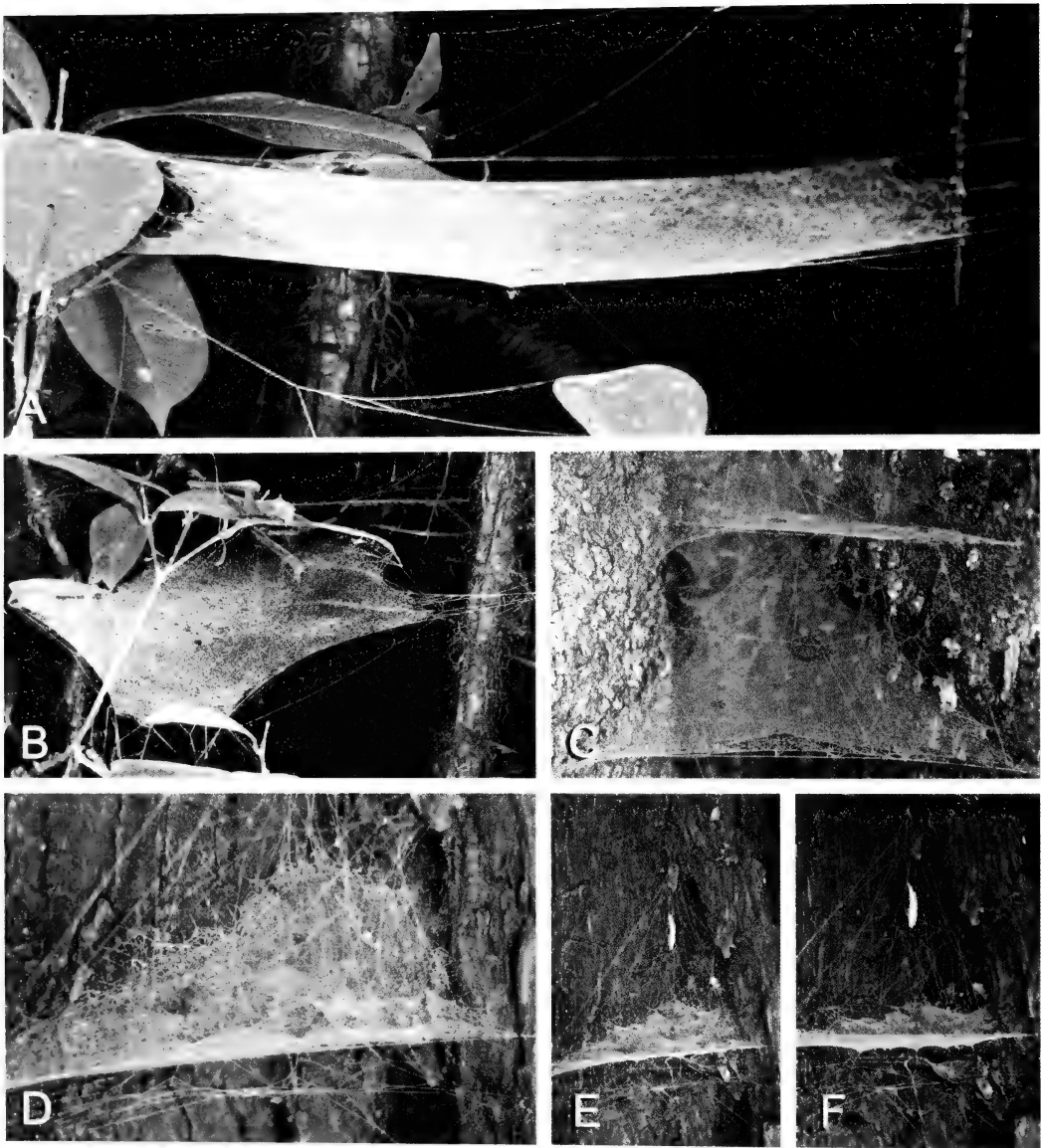


Figure 4. Cyatholipidae webs (2). (A, B) *Forstera* sp., female. Australia, New South Wales, Border Ranges National Park; note spider hanging under the sheet (DSC_3143. NEF, DSC_3142. NEF). (C) *Teemenaarus* sp., female, male. Australia, Queensland, Danbulla State Forest (GH020421_R08_30_AUS.TIF). (D–F) *Teemenaarus* sp., female, male. Australia, Queensland, Tamborine National Park (GH020417_R04_23_AUS.TIF, GH020417_R04_19_AUS.TIF, GH020417_R04_24_AUS.TIF).

1979; and in *Stemonyphantes blauveltae* Gertsch, 1951 (Hormiga, 2000). The near ubiquity of triads in linyphiids suggests that, contrary to some previous authors, linyphiid webs generally have sticky lines.

Study Goals

The present paper is largely descriptive rather than synthetic. It is based on a collection of field photographs made by

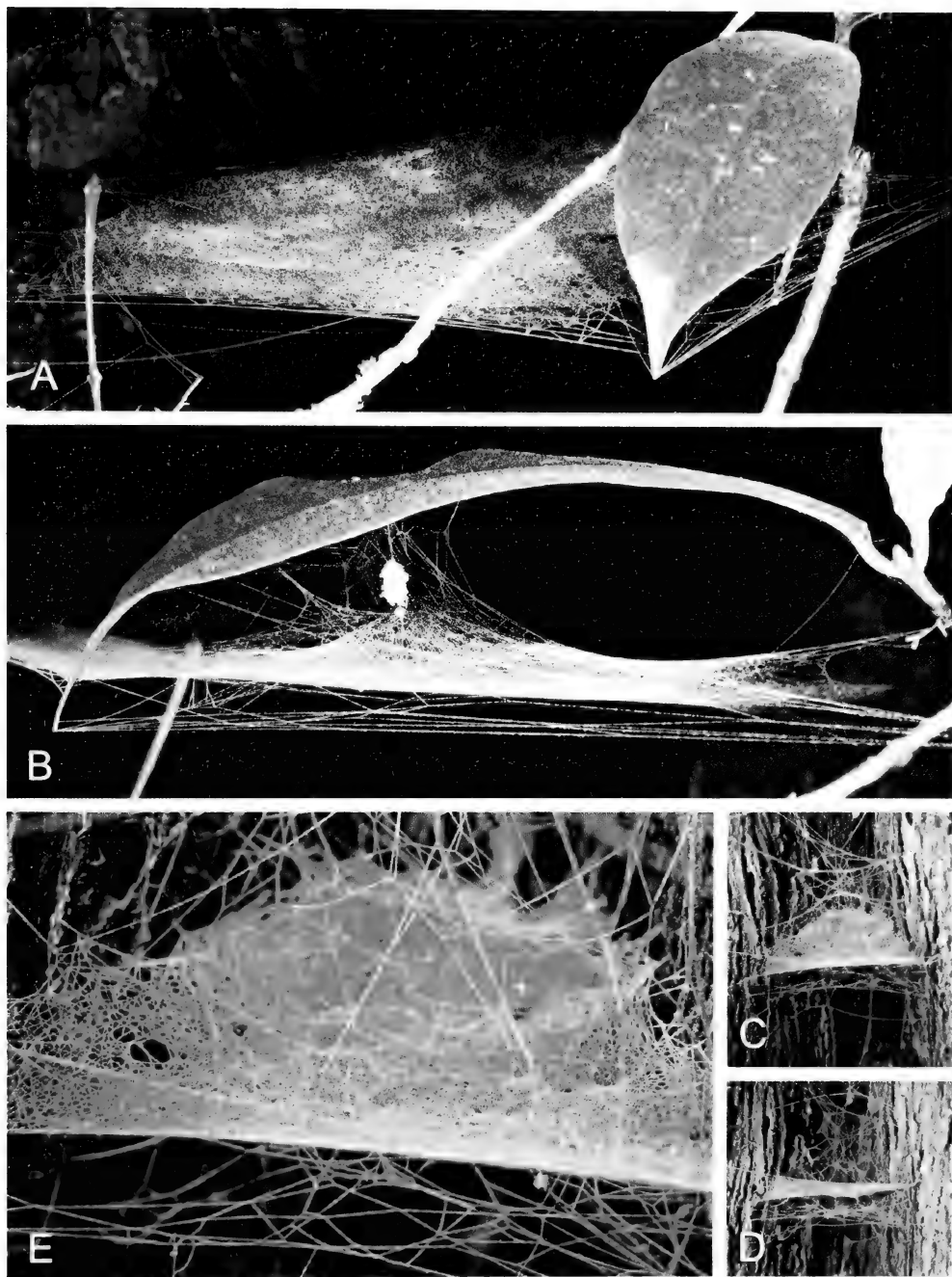


Figure 5. Cyatholipidae webs (3). (A, B) *Forstera* sp., female, Australia, New South Wales, Border Ranges National Park; note in panel B the egg sac covered in debris (DSC_3132.NEF, DSC_3135.NEF). (C–E) *Teemenaarus* sp. Australia, Queensland, Kuranda Environmental Park (GH920827_R05_28_AUS.TIF, GH920827_R05_31_AUS.TIF, GH920827_R05_33_AUS.TIF).

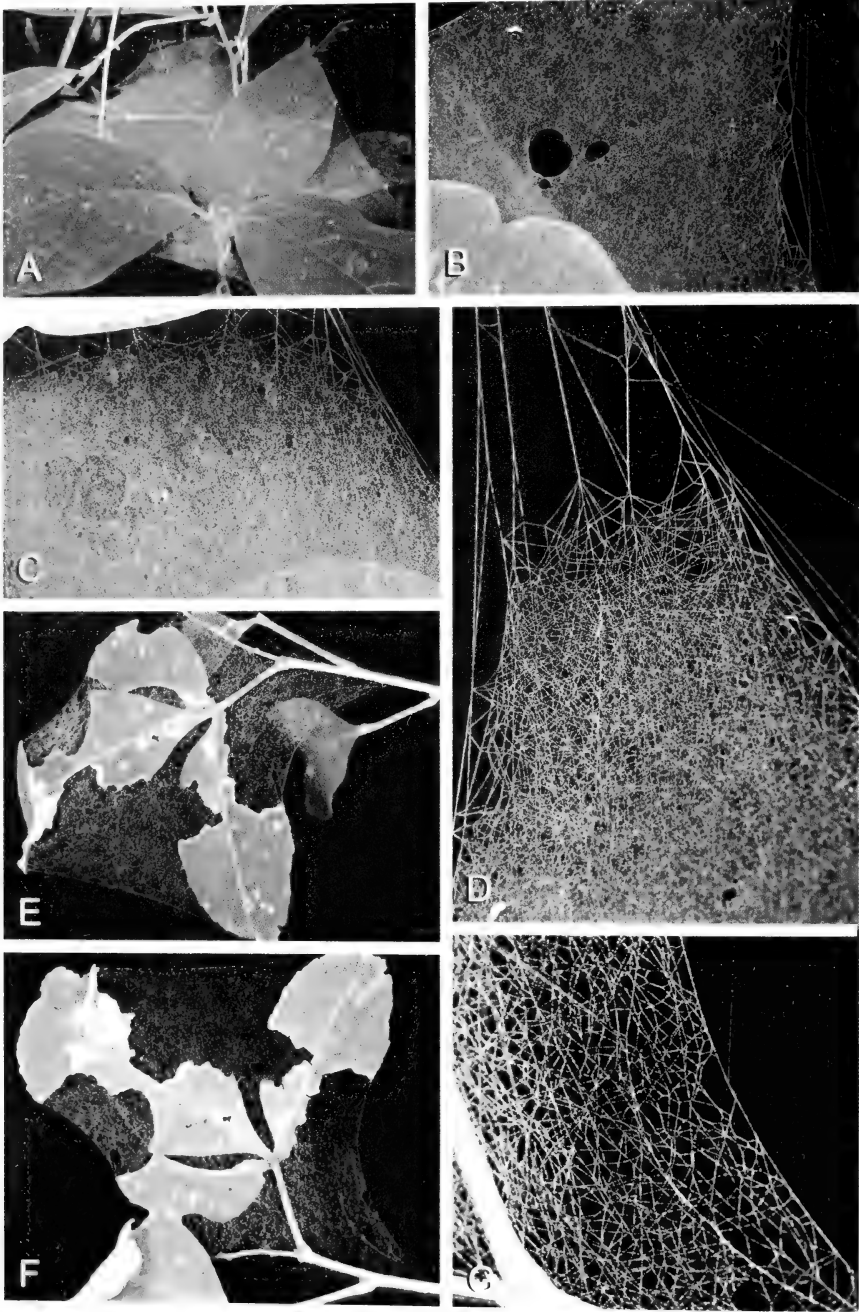


Figure 6. Cyatholipidae webs (4). (A) *Forstera* sp., female. Australia, Queensland, Atherton Tablelands (GH020420_R07_17_AUS.TIF). (B–D) *Forstera* sp., female with spiderlings. Australia, Queensland, Danbulla State Forest (GH020421_R08_18_AUS.TIF, GH020421_R08_17_AUS.TIF, GH020421_R08_20_AUS.TIF). (E–G) *Ulwembua* sp., female. South Africa, Sodwana Bay National Park (GH010406_R07_07_SAF.TIF, GH010406_R07_08_SAF.TIF, GH010406_R07_12_SAF.TIF).

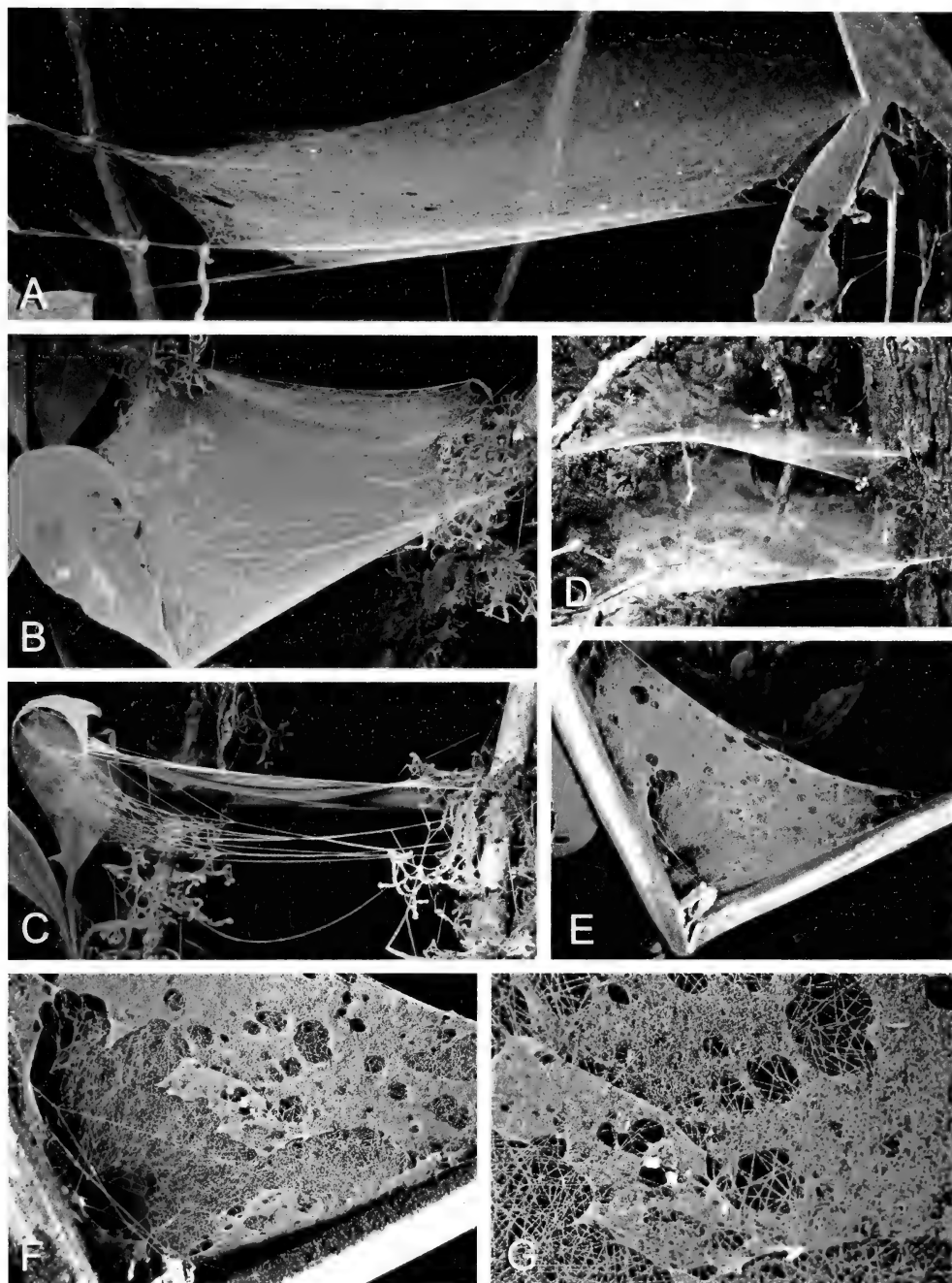


Figure 7. Cyatholipidae webs (5). *Wanzia fako* Griswold, 1998, Cameroon, Mount Cameroon. (A) Male (GH920126_R05_28_CAM.TIF). (B, C) Male (GH920127_R06_07_CAM.TIF, GH920127_R06_27_CAM.TIF). (D) Female, male (GH920122_R04_07_CAM.TIF). (E-G) Male (GH920124_R04_14_CAM.TIF, GH920124_R04_17_CAM.TIF, GH920124_R04_19_CAM.TIF).

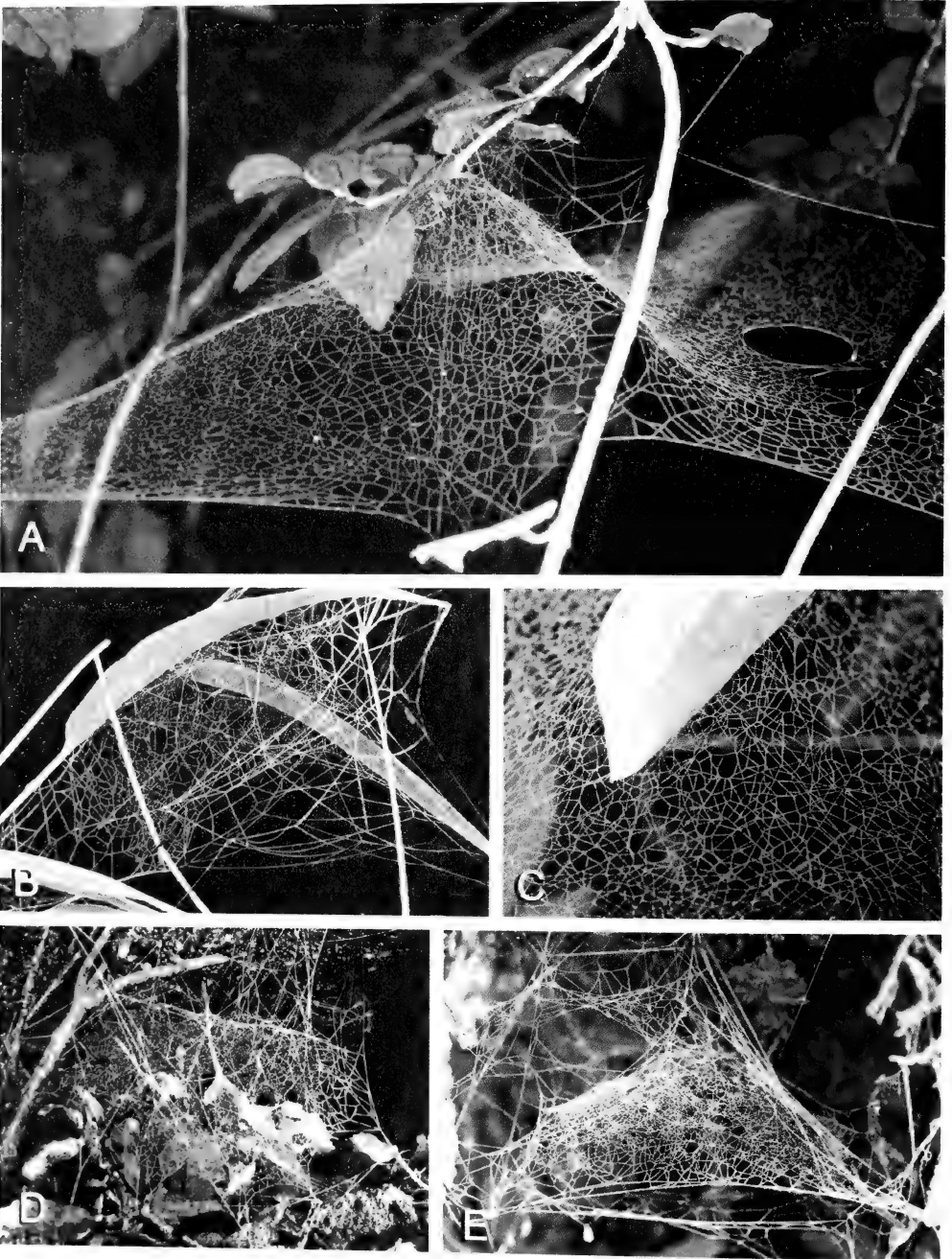


Figure 8. Physoglenidae webs (1). (A, C) *Chileotaxus sans* Platnick, 1990, male. Chile, Puyehue National Park (GH000730 R03 37 CHI.tif, GH001230 R03 04 CHI.tif). (B) *Chileotaxus sans*. Sex? Chile (DSC 2028.NEF). (D) *Mangua medialis* Forster, 1990, male. New Zealand (DSC 7925.NEF). (E) *Pahora* sp. New Zealand; photo courtesy of Charles E. Green (iCAsENT9062577 CRW 0363 CEG).

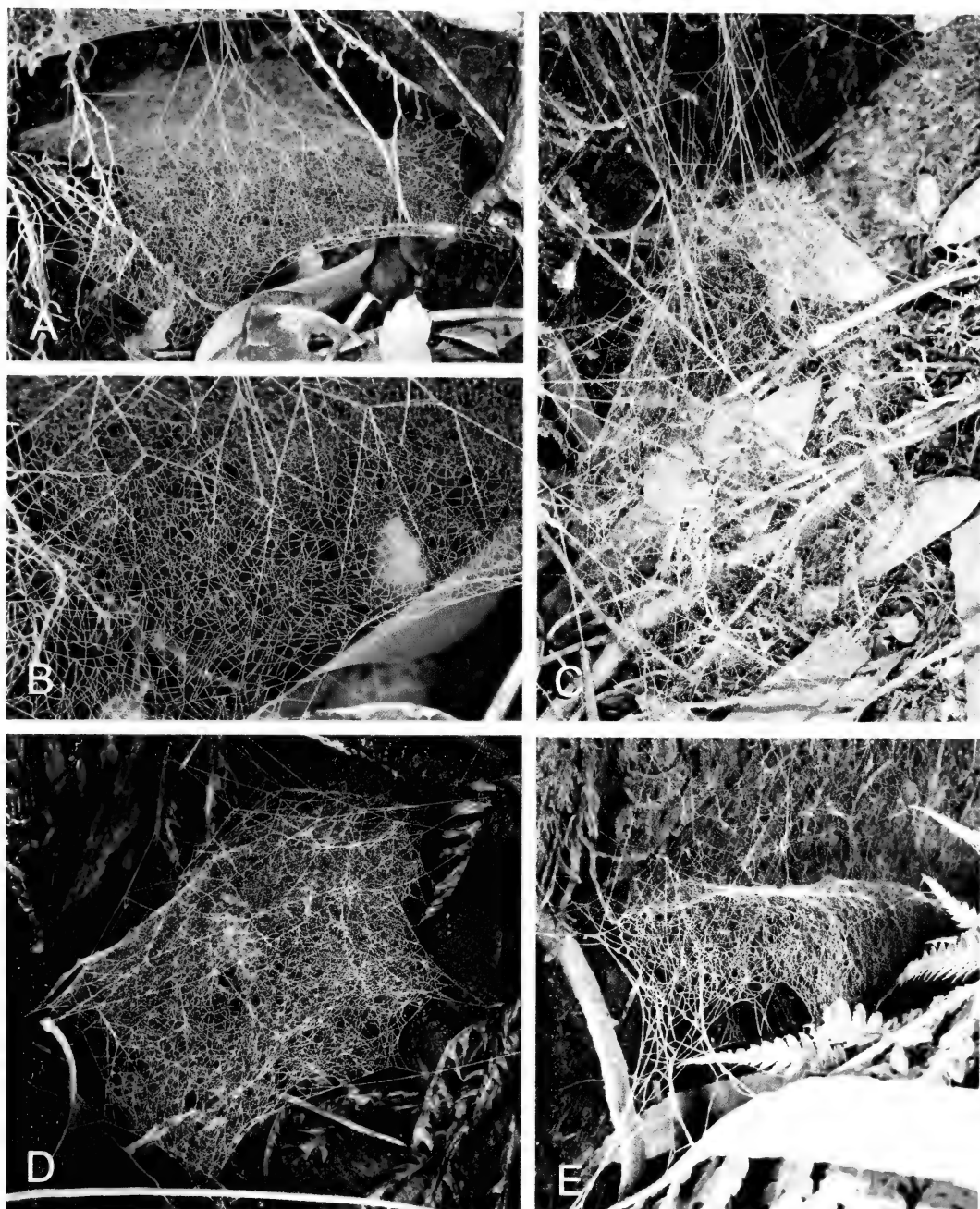


Figure 9. Physoglenidae webs (2). (A, B) *Physoglenes puyehue* Platnick, 1990, female. Chile, Puyehue National Park (GH001230_R03_14_CHI.tif, GH001230_R03_18_CHI.tif). (C) *Tupua* sp., female. Australia, Tasmania, Cradle Mountain-Lake St. Clair National Park (DSC_0264.NEF). (D) *Paratupua* sp., female. Australia, Victoria, nr. Warburton, O'Shannassy Aqueduct Trail, G. Hormiga (DSC_1392.NEF). (E) *Paratupua* sp., male. Australia, Victoria, Acheron Way, NE of Warburton (DSC_1532.NEF).

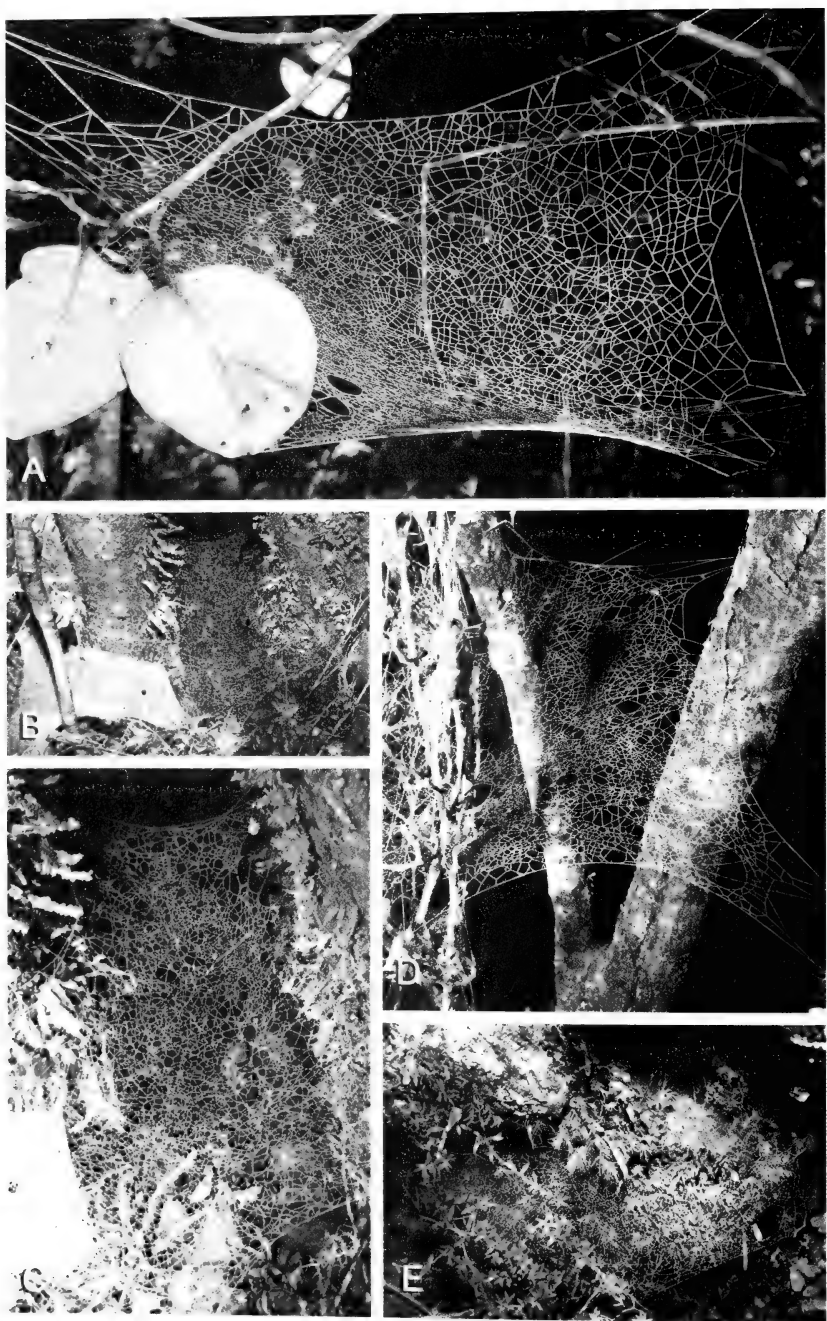


Figure 10. Physoglenidae webs (3). (A–E) *Runga* sp. New Zealand. (A) *Runga* sp., juvenile. New Zealand, South Island; Fox Glacier. Westland Tai Poutini National Park (DSC_7972.NEF). (B, C) *Runga* sp., male. New Zealand, South Island, Slab Hut Creek campground, nr. Reefton (note Stiphididae sheet web) (DSC_0064.NEF, DSC_0069.NEF). (D) *Runga* sp., female. New Zealand, South Island, Victoria Forest Park (DSC_0071.NEF). (E) *Runga* sp., female. New Zealand, South Island, Arthur's Pass National Park (DSC_7998.NEF).

G.H. over three decades in scattered parts of the world while carrying out other studies. The major goal is to expand taxonomic coverage: we triple the number of linyphioid species and more than triple the number of genera whose webs are documented. In most cases our descriptions of web traits are based on one or only a few webs rather than large samples of conspecific webs, so our samples are not adequate to document intraspecific variation; undoubtedly and unwillingly most if not all descriptions are overly typological. The considerable variation in web design in four species that have been studied in more detail (Hirschheimer and Suter, 1985; Rybak, 2007; Eberhard, 2022) suggests that substantial intraspecific variation is common in linyphiids.

The organization of this paper is adjusted to our small sample sizes. We do not try to characterize the web designs for any given species. Instead, the Results section first presents photographs of the webs of 112 species of linyphioids (in 39 genera) and then describes differences in the details of web designs, with photographs to illustrate. Additionally, we document webs of cyatholipids (eight species in five genera) and physoglenids (seven species in seven genera). In the Discussion we examine several evolutionary patterns by contrasting the ranges of variation in web designs in different genera, present a preliminary discussion of the possible functions of different web designs to speculate on why these diverse web forms have evolved, and note a suite of consistent linyphioid traits that we propose are associated with especially rapid attacks on prey. One ultimate intention is to discover web traits that may eventually provide useful information for grouping species and for tracing the evolution of linyphioid webs.

METHODS

We relied on photographs, both in our new descriptions and in obtaining data from

previous publications; we have not used drawings or verbal descriptions. Drawings of spider webs are usually more or less simplified, because depicting a web precisely, line by line is tedious and difficult, especially in three-dimensional webs. Additionally, because it is not clear at the moment which aspects of web structure may or may not prove to be important, drawings run the danger of omitting key traits. Verbal descriptions are even less satisfactory. There are simply not words in the language to describe adequately the complex arrays of lines in most linyphioid webs.

All web photographs were taken in the field. When several webs of what was presumed to be the same species were available, we selected webs to photograph according to the following criteria: the chosen web was representative ("typical") of the architecture of the presumed species, the web offered good background contrast, and the web did not seem to be damaged. In many species, we used only a single web, sometimes pictured in only a single photo, sometimes in several photos; we photographed a maximum of only eight different webs for any given species. We have thus undoubtedly underestimated intraspecific diversity. We mostly used webs of mature females (or occasionally penultimate females) and rarely of mature males (the possibility of ontogenetic changes in linyphioid web designs is, to our knowledge, nearly completely unexplored) (an exception is Rybak, 2007). Where possible, we noted the spider's resting site.

In nearly all cases the web was coated with cornstarch with a rubber "puffer" bulb similar to that described by Carico (1977) before being photographed (see Eberhard, 1976). The puffer consisted of an 85-mL rubber bulb (the type used for gas sampling or for pumping gas through an apparatus) combined with a piece of latex tubing. The latex tubing, ca. 7 cm long, was inserted into the bulb by means of a 3–4-cm piece of

hard plastic tubing. The distal tip of the latex tubing carries a 3-cm-long piece of hard plastic tube that was covered with several layers of nylon stocking to allow only fine grains of powder to be blown toward the web. The latex tubing made it possible to point its end toward specific areas that needed dusting and to avoid dusting background objects, to thus accentuate the contrast between web lines and their background in the photographs.

Most photographs were taken with a Nikkor 60-mm lens, most recently a Nikon AF-S Micro NIKKOR 60mm f/2.8G ED lens, illuminating the subject with a speed light (e.g., a Nikon SB28 or an R1 wireless close-up speedlight system) and with manual focus. Even in only moderately humid conditions, some cornstarch adhered to nonsticky lines, even after they were jarred, so we were not able to distinguish powdered sticky from powdered nonsticky lines (as noted above, probably a large fraction of the lines in the photos were weakly sticky). The weight of the powder undoubtedly caused some lines to sag unnaturally in the photos. In some cases, when the web was near the ground and when no photos were taken in horizontal view, it was not possible to rule out the possibility of a sparse tangle of lines under the sheet.

The figures are organized alphabetically by taxon, but the text of the Results section is organized by web designs. Our categories represent extensions and modifications of the lists of traits of Bristowe (1941) and Shinkai (1979). We do not want to imply that the order in which the traits are discussed or the groups of species that share particular traits reflect the phylogenetic relations between the species involved. We also do not attempt to cite all of the species in which any trait is visible in our verbal descriptions of web traits; we concentrate instead only on photos in which the trait is especially clear.

Numerous species are identified only to genus and some belong to genera that are

also yet to be described; we name these only with generic codes. For example, Australian genus 3 sp. GH02 denotes an undescribed species (GH02) from an undescribed genus (3) from Australia. All the species within a given genus have been checked against the congeneric species photographed to determine whether they are conspecific. Unless otherwise noted, voucher specimens are deposited in the Museum of Comparative Zoology (Harvard University) (see the Appendix for details). Figure legends (and the voucher label data given in the Appendix) provide the file name of all the images included in this publication (a total of approximately 1,600 web photographs were made). All counts of taxa are from World Spider Catalog (2022) Version 3 accessed on 4 May 2022.

RESULTS

Words are a problem. We are acutely aware that verbal descriptions often oversimplify and otherwise fail to do justice to the complex arrays of lines in spider webs. We also realize that the apparently qualitative distinctions that are made when one set of words is substituted for another (e.g., flat sheet vs. weakly domed sheet) are often inadequate to describe continuous, quantitative variations. Our admittedly imperfect solution has been to use photos to give the reader a key to what we want to indicate with the words in our descriptions. We have underlined terms for traits that are mentioned in the discussion of intrageneric variations and that represent possible characters of linyphioid webs.

Websites

We recognized several types of web sites. Webs on the substrate, as in *Mermessus tridentatus* (Emerton, 1882) (Fig. 47F), were attached at multiple points to the upper tips of moss plants near the surface of the ground and lacked clear frame lines. These webs appeared not to have a clearly

defined sheet; the web's upper surface was bumpy and formed by the lines that connected projecting tips of the substrate. *Erigone dentigera* O. Pickard-Cambridge, 1874 (Emerton, 1902), and *Erigone atra* (Nielsen, 1932) built similar webs lacking clear sheets on the substrate; Alderweireldt (1994) found that the webs of *Erigone atra* and *E. dentipalpis* (Wider, 1834) in cultivated fields were nearly always anchored to bare ground.

Webs near the substrate were just above the upper tips of the moss or objects in the leaf litter and were much more regular, usually forming flat sheets, as in *Tapinopa longidens* (Wider, 1834) (Fig. 76A) and *Neriene variabilis* (Banks, 1892) (Figs. 53A, C–F). We classified a sheet as near the substrate when the estimated distance between a sheet and the substrate below was less than about a sheet diameter.

Webs that were higher above the substrate were classified as elevated. We distinguished several types of elevated webs. In an elevated leaf web, one edge of the sheet abutted against the edge of a leaf. In some cases, as in *Agyneta* spp. (Figs. 11C, D, 12A–C), the density of lines in the sheet was higher at the edge of the leaf, indicating that the spider apparently rested under the leaf; in others, such as *Laminacauda* sp. “chdes” (Fig. 38F), the open mesh of the sheet near the leaf suggested that the spider instead rested under the sheet. In some, such as *Laminacauda malkini* Millidge, 1991 (Fig. 37A), the spider's likely resting place was uncertain.

In sheltered webs, one side was less than approximately one sheet diameter from a large nearby, more or less vertical object (e.g., a tree trunk, a dirt bank, etc.), as in *Labulla thoracica* (Fig. 31F). At the opposite extreme, no sheltering object was on any side of the web, as in *Novafrontina* sp. Brazil (Fig. 57C).

Often the sheltered side of the sheet had a denser mesh and was attached directly to the large object, as in *Laminacauda parvi-*

palpis Millidge, 1985 (Fig. 44E) and *Laetesia* sp. 1 (Figs. 33D, E). In some cases the density of the sheet did not vary dramatically, and its curvature or the positions of the tangles suggested that the spider rested on the sheet rather than the substrate; the sheet was simply attached on one side to a large object such as a tree trunk or a rock, as in *Neriene clathrata* (e.g., Figs. 51A, E), *Laminacauda magna* Millidge, 1991 (Fig. 40A) and *L. rubens* Millidge, 1991 (Figs. 38B–D). In contrast, the leaf shelter webs were attached to the underside of a large object such as a leaf or a branch, as in *Laetesia raveni* Hormiga & Scharff, 2014 (Figs. 32A–C, 33A, B). This species rested upside down under a leaf near the center of the sheet at the apex of the dome. When disturbed, the spider flattened its body against the leaf surface. Some species had webs with traits of both leaf webs and sheltered webs, as in *Laminacauda parvipalpis* (Fig. 44E).

The species of the plant may have been an important web site variable for the Australian plant-specific species *Laetesia raveni*. All but two webs in a series of 48 were built on two thorny plant species: most were on wait-a-while vines (*Calamus muel-leri* Wendland, 1875, Arecaceae) (Figs. 32B–E, 34A–C); others were on Gin's Whiskers (*Solanum inaequilaterum* Domin, 1929, Solanaceae) (Fig. 32A). The two exceptions, in Binna Burra (Lamington National Park), were webs built on other plant species that were in physical contact with one of the two thorny species (see Hormiga & Scharff, 2014). In a locality in Victoria, however, we found webs on non-thorny plants (Figs. 33A, B).

Most elevated webs were not associated with large objects, as, for instance, *Frontinella* spp. (Figs. 27A–D). In highly elevated webs the sheet was more than two sheet diameters above the ground or leaf litter, and was suspended from the leaves and branches of plants. An extreme case was *Pocobletus versicolor* (Millidge, 1991) (Fig.

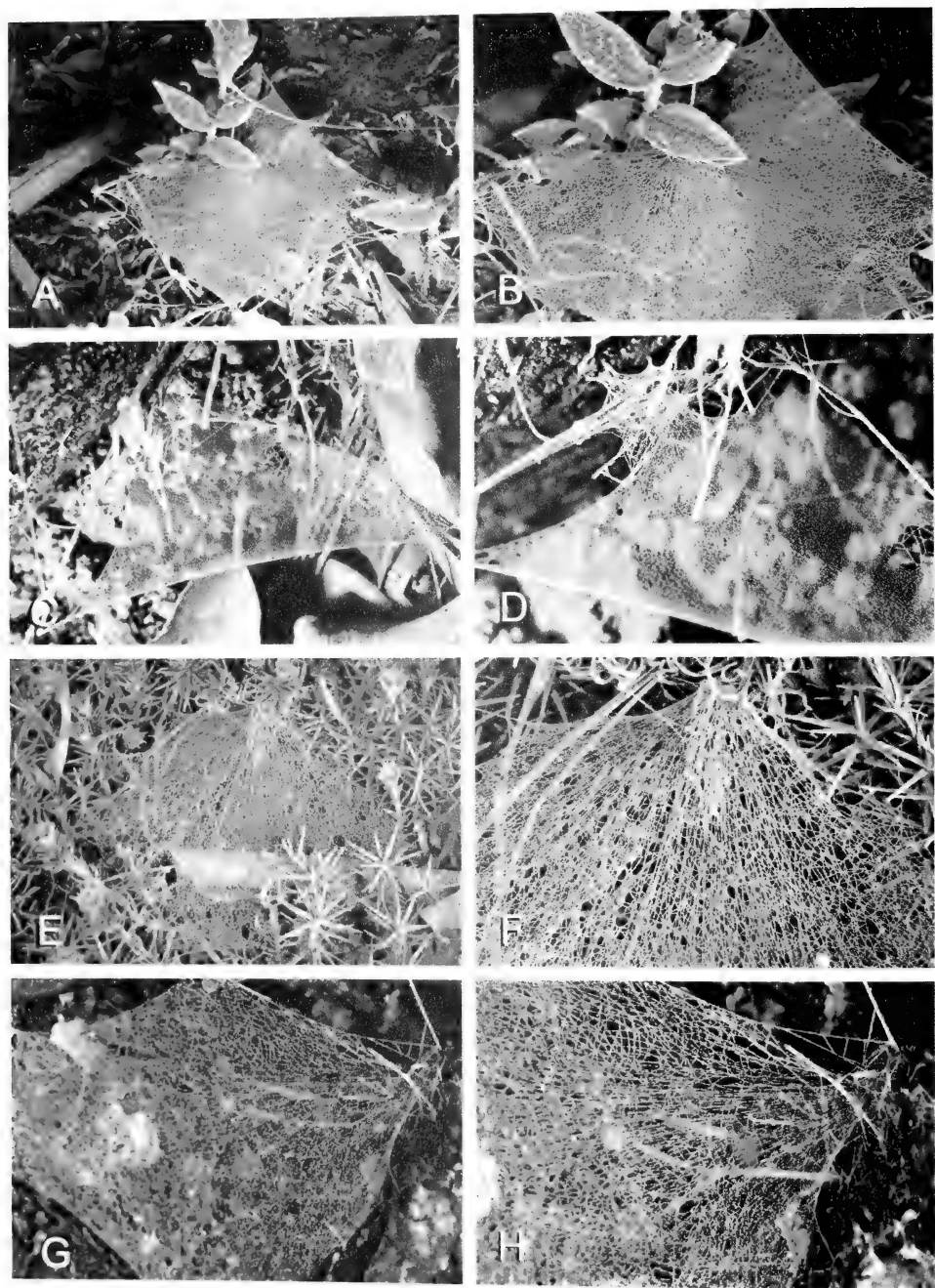


Figure 11. *Agyneta* webs (1). (A, B) *Agyneta* "CR01," female. Costa Rica, Estación Biológica La Selva (GH930404_R00_02_CRI_Meioneta.tif, GH930404_R00_07_CRI_Meioneta.tif). (C, D) *Agyneta* "CR01," female. Costa Rica, Estación Biológica La Selva (GH930402_R00_05_CRI.tif, GH930402_R00_10_CRI.tif). (E, F) *Agyneta semipallida* (Chamberlin & Ivie, 1944) female. USA, Maryland, Patuxent Wildlife Research Center (GH940519_R00_15_USA_Meioneta.tif). (G, H) *Agyneta* sp., subadult male. Colombia, Valle del Cauca, Farallones de Cali (GH980213_R03_12_COL_Meioneta.tif, GH980213_R03_14_COL_Meioneta.tif).

73E), in which the sheet was far from any substrate and was anchored by long lines at only four corners; the spider rested in the central portion of this sheet protected by the lower tangle (Fig. 73F).

Only very seldom did a web have any object protruding through either the sheet or the tangles of a web. In other words, web sites almost always had open spaces at least the size of a web. One exception was a *Juanfernandezia melanocephala* Millidge, 1991, sheet with a stem protruding through it (Fig. 29C) (an obstructed sheet). The only linyphiid species we know of in which objects (thin leaves) regularly protrude through the sheet is *Nerienne coosa* (Eberhard, 2022). Twigs and leaves that penetrate sheet webs are not uncommon in species in other families such as Lycosidae, Zoropsidae (Eberhard and Hazzi, 2017), and Hahniidae (Eberhard, 2019). In sum, linyphiids consistently chose web sites with sufficient objects nearby to which to attach their webs and that had a completely open space in which the web would be built.

Sheet Form

All of the webs described here except those on the substrate had more or less horizontal sheets that were at least moderately dense. A “sheet” was an approximately planar array of lines (sometimes strongly curved upward or downward) where coplanar lines appeared to be denser than elsewhere; only occasionally was it difficult to distinguish a tangle from a sheet (e.g., some of the webs of *Laminacauda ansoni* Millidge, 1991, Figs. 36A–F). The sheets were “dense” compared with the open mesh sheets in other families such as Psechridae (Robinson and Lubin, 1979; Eberhard, 1987) and Austrochilidae (Lopardo et al., 2004), often having lines so dense that they were difficult to distinguish from each other in the photos. One linyphiid, *Bathypantes eumenis* (= *simillimus*), builds sparse webs that lack sheets

(Rybák, 2007). These webs, which were discovered in captivity, were so sparse and irregular in form that it is not clear that they would have been recognized as prey capture webs in the field. The lack of such webs in our study may thus be an artifact of the difficulty of distinguishing such sparse webs from incidental, sparse accumulations of drag lines in the field.

Cup-shaped. The outer edges of cup-shaped sheets sloped upward more or less symmetrically on all sides from a more or less central low area. The angles of the slopes varied. In weakly cup-shaped sheets, the upward slant was barely perceptible, as in *Laminacauda tuberosa* Millidge, 1991 (Fig. 39H), *Acroterius* sp. (Fig. 79F), and *Nerienne clathrata* (Figs. 51A, E); weak slants verged on flat, as in *Acroterius* sp. (Fig. 79E). In moderately cup-shaped sheets the angle was clear but not strong, as in *Novafrontina* sp. (Fig. 57B). The angle of curvature was more acute in strongly cup-shaped sheets, as in *Pocobletus* sp. GH02 (Figs. 74C, D). In asymmetrical cup-shaped sheets, one edge of the sheet was much higher than the others and formed a nearly vertical wall, as in *Nerienne* sp. GH03 (Figs. 52A, B) and *Acroterius* spp. (Figs. 78, 79B); in other tilted asymmetrical cup-shaped sheets the entire cup was tilted to the side, as in *Laminacauda* sp. “fPC” (Fig. 43A).

Double Sheets. Some webs with a cup-shaped principal sheet had a second, lower sheet just below that was also cupped-shaped. Some webs barely had enough space between the two sheets for the spider to move, as in *Acroterius* sp. (Figs. 78, 79C); the space was much greater in others, such as *Mecynidis* sp. (Figs. 47A–C) and *Frontinella* spp. (Figs. 27A–D). The distinction between a sparsely meshed lower sheet and a lower tangle was not always clear, as in *Laminacauda* “fCh” (Fig. 43E). Flat sheets also occasionally had a second sheet-like structure in the lower tangle, as in *Mecynidis* sp. (Figs. 47A–C). In contrast, no web

with a dome-shaped sheet had a second sheet. In one web of *Mecynidis* sp. it appeared that a leaf replaced the lower sheet (Figs. 47D, E).

Lower sheets were always less densely meshed than the principal sheet. Some lower sheets were relatively small and covered only the lowermost portion of the principal sheet, as in *Acroterius* sp. (Fig. 78), and *Nerience digna* (Keyserling, 1886) (Figs. 50G, H). Other lower sheets were nearly as wide as the principal sheet, as in *Frontinella* spp. (Figs. 27A–D).

Trough-shaped. A male of *Agyneta* sp. Guyana built a unique trough-shaped sheet just above the upper surface of a longitudinally curved leaf on the forest floor. The elongate sheet, about 8 cm long, approximated the lower half of a cylinder laid on its side just above the surface of the leaf (Fig. 12F). The sheet's lateral edges slanted upward, but not its ends. The upper tangle of this web spanned the space between the lateral edges of the leaf (Figs. 12D, E), with a much smaller lower sheet under the main sheet.

Dome-shaped. The outer edges of dome-shaped sheets sloped downward more or less symmetrically from a more or less central area. The angle of the slope varied widely. In weakly dome-shaped sheets, the slant was barely perceptible, as in *Diplothyron diana* Silva-Moreira & Hormiga, 2022 (Fig. 20D), and *Laminacauda propinqua* Millidge, 1991 (Fig. 39G), and verged on flat, as in *Nerience variabilis* (Figs. 53D–F). In moderately dome-shaped sheets, the angle was clear but more obtuse, as in *Laetesia raveni* (Fig. 33B). The angle of curvature was more acute in strongly dome-shaped sheets, as in *Nerience albolimbata* (Karsch, 1879) (Figs. 50A–D), and *N. litigiosa* (Keyserling, 1886) (Figs. 53G, 56). Only rarely a sheet was dome-shaped in one portion and saddle-shaped in another, as in *Nerience helsdingeni* (Locket, 1968) (Figs. 55C, D). The surfaces of domes were relatively smooth with small upward-pro-

jecting dimples, as in *Diplothyron* sp. (Fig. 20D). In asymmetrical dome-shaped sheets one side of the dome extended much farther downward than the others, as in *Putaoa seediq* Hormiga & Dimitrov, 2017 (Figs. 75C, D), and *Laetesia* sp. GH02 (Figs. 34D, E); in extreme cases the extended side formed a vertical wall, as in *Pimioa cthulhu* Hormiga, 1994 (Figs. 64A, B).

In dome + tube webs, the upper tip of a clear dome extended to form a short tube; some tubes led to the substrate, as in *Laminacauda ansoni* (Fig. 36D), and other tubes of this same species ended in the upper tangle (Fig. 36A).

Flat. In flat sheets, the entire sheet was in more or less the same plane. Many flat sheets were approximately horizontal, as in *Tenuiphantes flavipes* (Blackwall, 1854) (Fig. 77A), *Walckenaeria*(?) sp. (Figs. 77D, E), and *Tapinopa bilineata* Banks, 1893 (Fig. 76D), but some flat sheets were substantially inclined, as in *Mecynidis* sp. (Fig. 47B). Sheets that sagged slightly, apparently because of their coat of powder, were classified as flat. Some flat sheets had lines attached to them that pulled the sheet slightly upward, producing a bumpy flat sheet, as in *Nerience variabilis* (Figs. 53D–F) and *Nerience* sp. GH02 (Figs. 53A, B). The edges of some flat sheets curled slightly upward, as in *Laminacauda tuberosa* (Fig. 39H, left).

Tent-shaped. In a ridge tent sheet, an uppermost central ridge, supported by a single long line from one edge of the web to the other, slanted upward at one end toward a nearby large leaf and sloped downward on both sides of the central ridge, as in *Laminacauda* sp. “chdes” (Fig. 38F).

Sandwich. Sandwich sheets, as in *Tapinopa bilineata* (Fig. 76D) and *Laminacauda magna* (Fig. 41D), consisted of a pair of more or less flat parallel sheets, one above the other. They were attached near the base of a tree and their edges were loosely

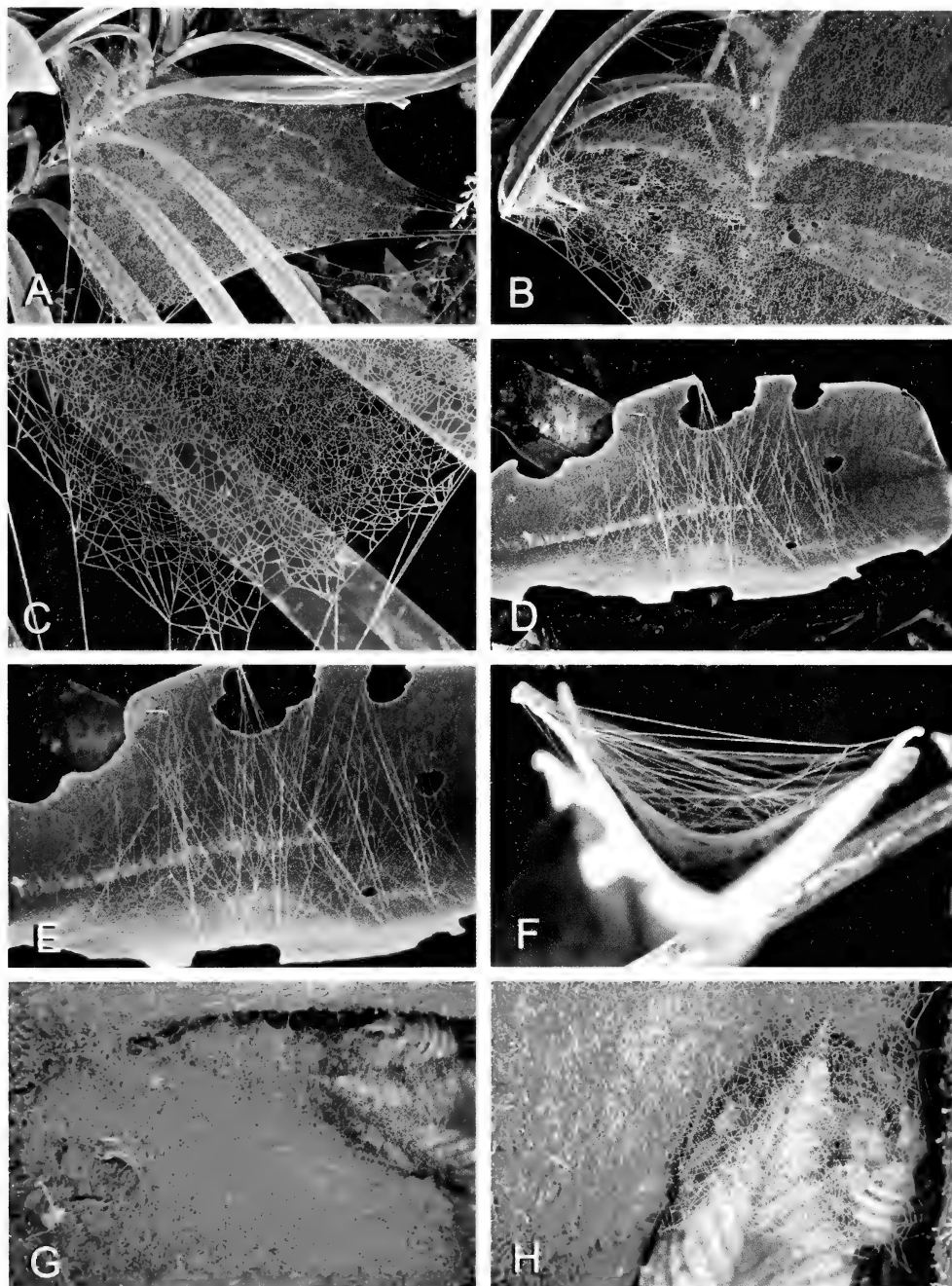


Figure 12. *Agyneta* webs (2). (A–C) *Agyneta* sp. HI02, female. USA, Hawaii, Kauai (GH950816_R06_13_HAW_Meioneta.tif, GH950816_R06_15_HAW_Meioneta.tif, GH950816_R06_18_HAW_Meioneta.tif). (D–F) *Agyneta* nr. *luctuosa*, male. Guyana, Gunn's Landing Strip (GH990710_R04_01_GUY_Meioneta.tif, GH990710_R04_05_GUY_Meioneta.tif, GH990710_R04_07_GUY_Meioneta.tif). (G, H) *Agyneta micaria* (Emerton, 1882), female. USA, Maryland, Patuxent Wildlife Research Center (GH940602_R00_28_USA_Meioneta_sp2.tif, GH940602_R00_29_USA_Meioneta_sp2.tif).

joined, thus enclosing the spider, which walked on the underside of the upper sheet.

Saddle-shaped. Saddle-shaped sheets resembled dome-shaped sheets but with one side sloping upward, as in *Neriere helmsdingeni* (Fig. 55D).

Tube at the Edge. Some sheets were continuous with the wall of a tube at the edge located at one edge of the sheet, as in *Putaoa seediq* (Figs. 75C–F) and (possibly) in *Pimoa cthulhu* (Fig. 64C). In *P. seediq* the tube served as the spider's retreat. Funnel-like silk tubes leading into a retreat were also common in *Orsoniwell* species (e.g., *O. polites* Hormiga, 2002; Figs. 62B, C, E). Tubes were not always easy to distinguish from runways (below).

Complex Sheet Form. A few complex sheets had forms that did not fit easily into the preceding categories, as in *Laperousea* sp. GH01 (Fig. 45E) and Australian genus 3 sp. GH01 (Figs. 18A, B).

Naked and Nearly Naked Sheets

Many naked sheets and nearly naked sheets had few or no lines either above or below. Naked sheets were never cup- or dome-shaped. The association between curved sheets and lines above and below it was probably because the sheet could only be pulled into a curve by additional lines out of the sheet's plane.

Naked sheets varied in several ways. Some were near the substrate, as in *Himalaphantes* sp. (Figs. 28D, E), *Tenuiphantes flavipes* (Figs. 77A–C), *Agyneta* sp. Maryland (Figs. 12G, H), *Sphecozone ardens* Millidge, 1985 (Fig. 63B), and *Australolinyphia remota* Wunderlich, 1976 (Fig. 19G). (About 25 other webs of this species also consisted of nearly naked sheets.) Others were elevated, as in *Agyneta* spp. Colombia and Hawai'i (Figs. 13D, E), *Laminacauda malkini* (Fig. 37A), *Dubiaranea* sp. Ecuador (Figs. 24D, E), and *Grammonota* sp. (Fig. 28A). Some were sparsely meshed, as in *Laminacauda malki-*

ni (Fig. 37A), whereas others were densely meshed, as in *Agyneta* sp. CR01 (Fig. 11B) and *Grammonota* sp. (Fig. 28A). A few nearly naked sheets near the substrate had patches of slime, as in *Laminacauda magna* (Figs. 42A, B). (We inferred that the slime was from the spider and not some other agent, such as a snail, from the pattern and distribution of the slime.) A more extreme case was *Tapinopa longidens*, whose naked sheet was covered with slime (Fig. 76A). Nielsen (1932) and Bristowe (1941, 1958) also described a slime-covered sheet in this species; web photos of this species (Shinkai, 1979; Shinkai and Takano, 1984) also show tiny naked sheets near the ground that were not obviously shiny, but it is possible that a shine would only be apparent at certain angles of illumination, so a slimy surface cannot be confidently ruled out). The stickiness of the glistening silk in one *L. magna* sheet was no different from that of the adjacent sheet, as assessed by light contact with the blunt metal end of a mechanical pencil. The majority of the many *L. magna* webs examined lacked slime, so slime is an uncommon feature in this species.

Patterns of Lines in Sheets

Density. The "mesh" of a sheet refers to the density of lines in the sheet. Densities of lines in the sheet ranged from sparse, as in *Laminacauda ansoni* (Figs. 36D, E), Australian genus 2 sp. GH01 (Figs. 14C–F) and *Dubiaranea lugubris* Millidge, 1991 (Figs. 22C, D), to medium dense, as in *Dubiaranea insulana* Millidge, 1991 (Figs. 23C–E) and *Dubiaranea fulgens* (Millidge, 1985) (Fig. 22A), to dense, as in *Floronia bucculenta* (Fig. 26D), *Agyneta* sp. CR01 (Fig. 11B), and (at least in the central area) *Dubiaranea* sp. Ecuador (Fig. 25C) and *Dubiaranea* sp. Costa Rica (Fig. 22F). Very dense sheets were those in which individual lines could not be easily distinguished, as in *Pocobletus versicolor* (Figs. 73C, E).

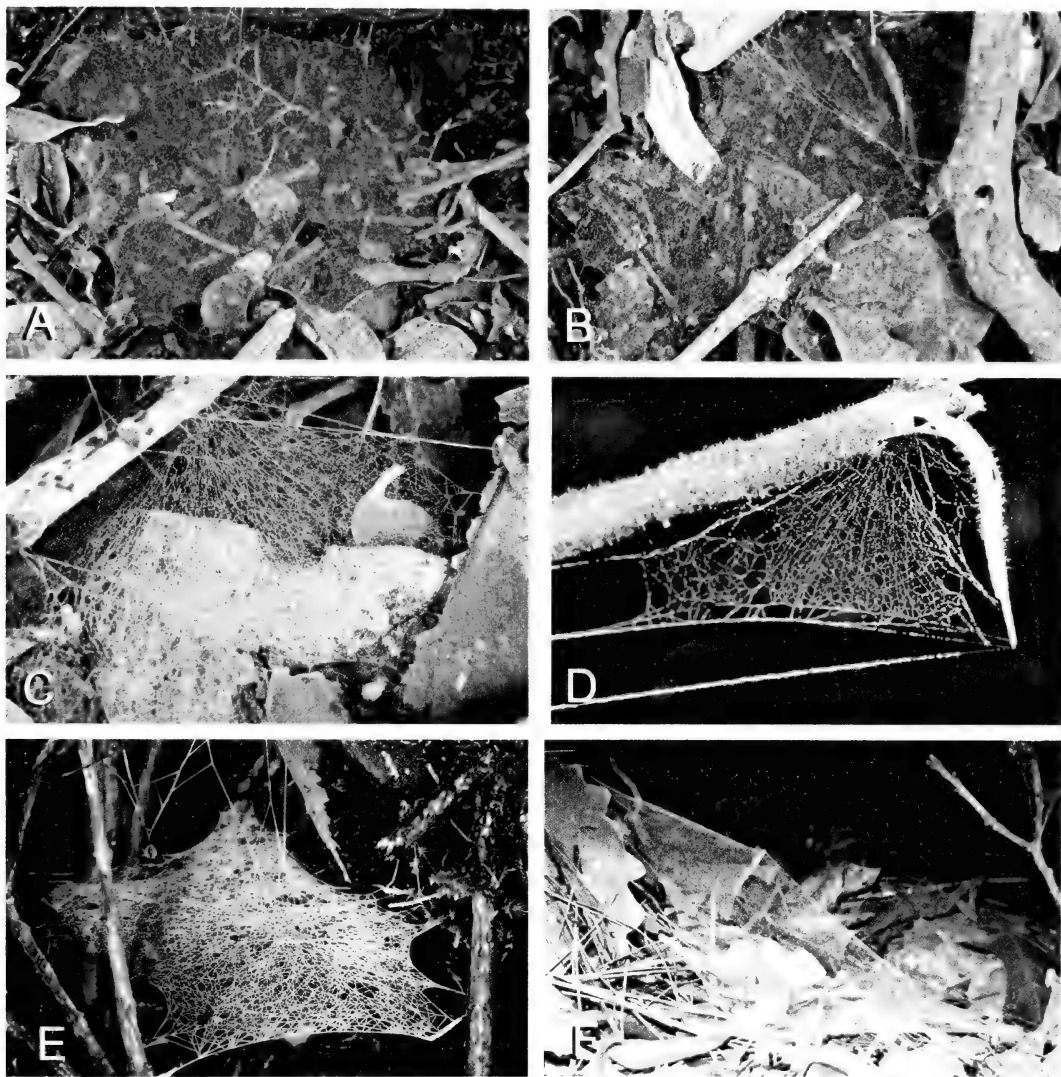


Figure 13. *Agyneta* webs (3). (A, B) *Agyneta* sp. females. South Africa, Sodwana Bay National Park (GH010407_R08_02_SAF_Meioneta.tif, GH010407_R08_04_SAF_Meioneta.tif). (C) *Agyneta* sp., male (same species as above). South Africa, Sodwana Bay National Park (GH010404_R06_13_SAF_Meioneta.tif). (D) *Agyneta* sp., male. Colombia, Valle del Cauca, Farallones de Cali (GH980213_R03_04_COL_Meioneta.tif). (E) *Agyneta* sp. H101, female. Hawaii. Oahu, Mt. Ka'ala (GH950813_R04_01_HAW_Meioneta.tif). (F) *Agyneta* sp. (undet.), female. USA, North Carolina (GH910622_R00_17_USA_Meioneta.tif).

The density of lines in the sheet often varied in different parts of the sheet and was lower near the edge than it was in the rest of the sheet in *Dubiaranea* sp. Costa Rica (Fig. 22F), *Dubiaranea* sp. Ecuador (Figs. 23F, G), *Labulla thoracica* (Fig.

31G), and *Laminacauda magna* (Fig. 42A). Greater density at the edge of the sheet that abutted broadly with a sheltering object, which occurred in *Laminacauda magna* (Fig. 41C, top right), *Laminacauda* sp. (Fig. 44E), *Putaoa seediq* (Fig. 75A),

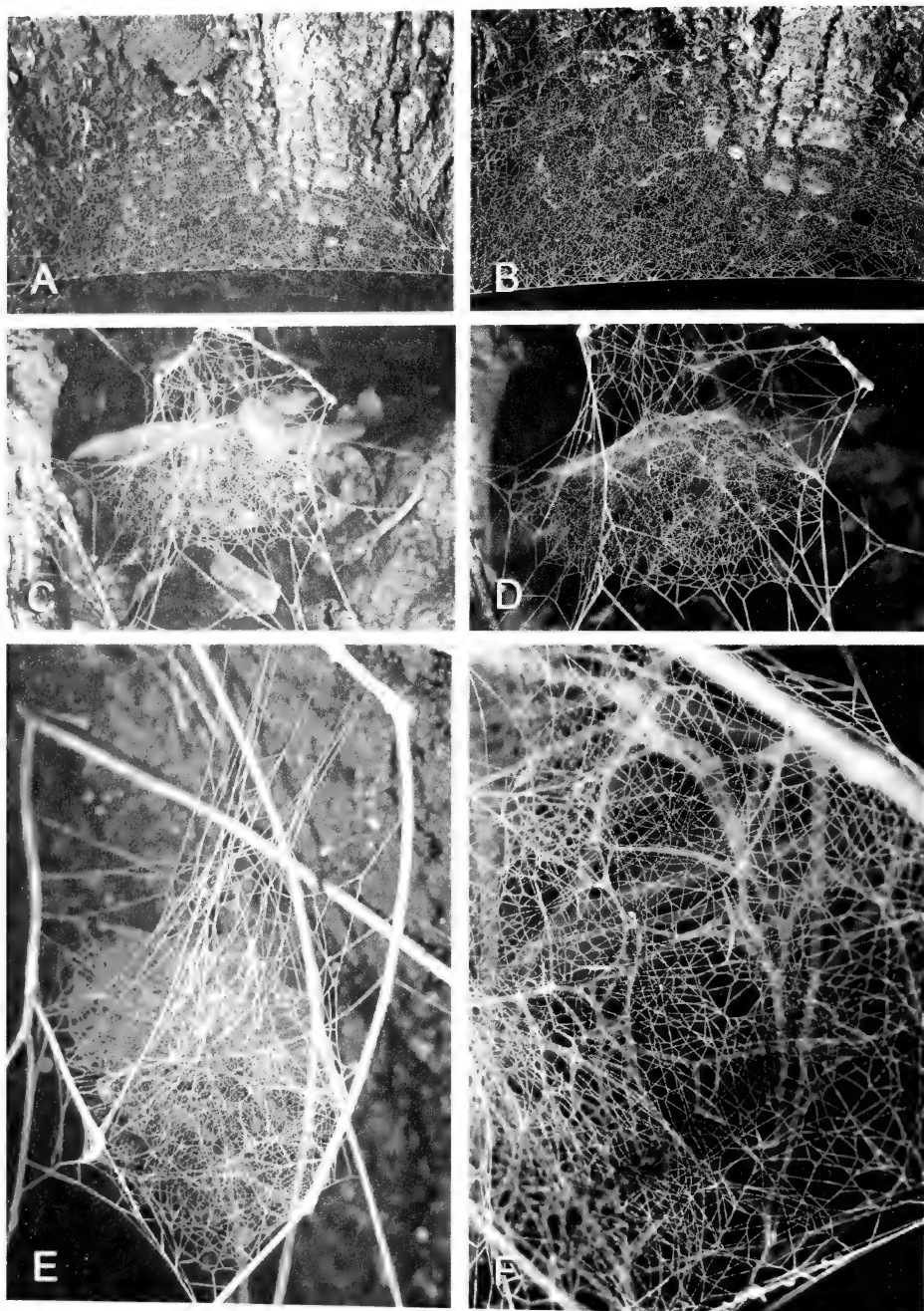


Figure 14. Australian genera 1 and 2 webs. (A, B) Australian genus 1 GH06, female. Australia, Tasmania, Mt. Field National Park (DSC_1585.NEF, DSC_1587.NEF). (C, D) Australian genus 2 GH01, female. Australia, Queensland, Lamington National Park (GH920416_R03_07_AUS.tif, GH920416_R03_09_AUS.tif). (E, F) Australian genus 2 GH01, female. Australia, Queensland, Lamington National Park (GH920719_R01_24_AUS.tif, GH920719_R01_26_AUS.tif).

Orsonwelles macbeth Hormiga, 2002 (Fig. 60G, upper left), and *O. polites* (Fig. 62B), may have been associated with the spider resting at or just beyond the edge of the sheet, but further observations will be needed to test this idea. Differences in density could result from lines having accumulated near the retreat in older sheets. Thus, the sheet of *Pityohyphantes costatus* (Hentz, 1850) shown in Figures 65A–C, which abutted broadly with the substrate where the spider rested but had no local increase in density, may have been recently built (this web was photographed at about 9 p.m.).

Lines Radiating from a Corner. Many lines radiated from one corner of the sheets (where the spiders were usually found) in *Agyneta* spp. Colombia, Costa Rica, Maryland, Hawaii, and South Africa (Figs. 11, 12A, B, 13B–D); this pattern did not occur in sheets of other *Agyneta* species from Hawaii (Fig. 13E) and Maryland (Figs. 12G, H). This radiating pattern has not been seen outside the genus *Agyneta*.

Frame Lines. Often sheets had long frame lines at their edges, as in *Grammonota* sp. (Fig. 28A), *Floronia bucculenta* (Figs. 26D, E), and *Bathypantes pallidus* (Fig. 20A). Other sheets had no frame lines, and the edge of the sheet was anchored to the substrate by many separate lines, as in *Novafrontina* sp. Brazil (Fig. 57C) and *Australolinyphia remota* (Fig. 19E). In some cases, as in *Walckenaeria*(?) sp. (Figs. 77D, E), the same sheet lacked frame lines at one edge but had clear frame lines at another. In *Sphecozone ardens* (Fig. 63B) the frame lines were all relatively small. Another variant, seen in *Laminacauda magna* (Fig. 42A) and Australian genus 1 spp. GH03 and GH05 (Figs. 17B, E, F), had long marginal pseudo-frame lines at the extreme edge; the mesh of the sheet was so sparse at the edge, and these lines supported very few sheet lines.

In some sheets with frame lines, many lines in the sheet made V-shaped intersec-

tions with the frame, as in *Agyneta* sp. Guyana (Fig. 12H), *Diplothyron* sp. Costa Rica (Fig. 20G), and *Dubiaranea* sp. Ecuador (Fig. 24E). V-shaped attachments presumably resulted when, during sheet construction, the spider attached the line it was laying to the frame and then turned back sharply (Benjamin and Zschokke, 2004). Nearly identical patterns occur at the edges of some pholcid and theridiid webs (Eberhard, 1992, 2020), and direct behavioral observations of one pholcid confirmed that the “V” patterns were also produced when the spider turned back after reaching the edge of the sheet (Eberhard 1992). In other webs, sheet lines made few or no V-shaped intersections with the frame, as in *Bathypantes pallidus* (Figs. 20B, C), *Labulla thoracica* (Fig. 31B), and *Dubiaranea* sp. Costa Rica (Fig. 22F). Some sheets had a mix of multiple V-shaped intersections and few V-shaped intersections on different frame lines, as in *Pityohyphantes costatus* (Fig. 65A, right and left, respectively), Australian genus 1 sp. GH03 (Figs. 17A–C), and *Labulla thoracica* (Fig. 31G, left and lower edges).

Some sheets had secondary frame lines, relatively straight lines near the edge of the sheet that were attached at both ends to a frame line and that had multiple sheet lines attached to them, as in the near edge of the *Orsonwelles polites* web in Figure 62D. The edge of the dense central portion of the sheet was thus scalloped and was attached to a few, perhaps stronger frame lines that formed a second, more peripheral edge.

Parallel Lines. Some sheets had sets of two or more nearby parallel lines that ran nearly parallel to each other for short distances, sometimes straight and sometimes in curves, as in *Diplothyron* sp. (Fig. 20G) and *Agyneta* sp. Maryland (Fig. 12H). Perhaps the most striking parallel lines were the pairs of sticky lines that wandered across the sheet of *Dubiaranea lugubris* (Figs. 22C, D). We do not know whether

these pairs were laid simultaneously or sequentially.

Skeleton Web Lines. Some sheets included possible skeleton web lines that were longer and straighter than other lines in the same sheet, as in *Labulla thoracica* (Fig. 31G); some skeleton web lines were approximately parallel to a nearby frame line, as in *Dubiaranea* sp. Ecuador (Fig. 25C). In contrast, no possible skeleton web lines were visible in other sheets, as in Australian genus 1 spp. GH03 and GH05 (Figs. 17B, F).

Repairs. Apparent repairs of holes in the sheet occurred in several species, including *Floronia bucculenta* (Fig. 26E), and *Orsonwelles falstaffius* Hormiga, 2002 (Figs. 59D, E). One web of *Tenuiphantes flavipes* (Figs. 77A, C) had three zones with different densities, perhaps corresponding to successive repairs.

Dimples. A dimple was where a “tensor line” (Suter, 1984) that attached more or less perpendicularly to the sheet pulled the sheet out of the plane of nearby portions of the sheet. Most tensor lines were attached to tangle lines, but the lines pulling the sheet into dimples ran directly to the substrate in *Neriere montana* (Nielsen, 1932, vol. 1, fig. 59).

Downward-directed dimples pulled the sheet downward in areas where the sheet curved upward, as in cup-shaped sheets in *Frontinella* spp. (Figs. 27A–D), *Dubiaranea* Trinidad and Tobago (Figs. 24B, C), and *Acroterius* sp. GH02 (Fig. 78). Upward-directed dimples pulled the sheet upward in some dome-shaped sheets, as in *Diplothyron diana* (Fig. 20D), *Laetesia raveni* (Fig. 34B), and *Laetesia* sp. GH02 (Fig. 34E). These dimples were not as pronounced as many downward dimples and were sometimes nearly imperceptible, as in *Neriere litigiosa* (Fig. 53G). The inverse relation between the directions of dimples and the local curvature of the sheet is logical if dimples are sites where the sheet is being pulled toward a tangle (Suter, 1984) (see

Discussion). There were, however, exceptions. Some dimples occurred in relatively flat sheets, as in *Neriere oxycera* Tu & Li, 2006 (Fig. 54C), and *Laperousea* sp. GH1677 (Fig. 45C); as just noted, some strongly curved sheets lacked large dimples, as in *Neriere litigiosa* (Fig. 53G).

Some dimples were large, as in *Laperousea* sp. GH01 (Fig. 45F), *Neriere clathrata* (Fig. 51B), *Neriere oxycera* (Figs. 54B, C), and *Linyphia triangularis* (Fig. 46C). Others were of more moderate size, as in Australian genus 4 (Figs. 19A–C) and *Laetesia* sp. GH02 (Fig. 34E), and some were small and barely perceptible, as in *Neriere litigiosa* (Fig. 53G) and *Dubiaranea distincta* (Nicolet, 1849) (Fig. 21E). Other less pronounced local irregularities in the slope were abundant in some sheets but were not counted as dimples. Concentrations of tangle lines, curves in the sheet surface, and lack of depth of field probably obscured dimples in some web photos.

Runways. A runway (termed a “funnel” by Hormiga, 2002) was a relatively densely meshed extension of the edge of a sheet to a sheltering object like a tree trunk where the spider waited. Runways were present at the edges of the sheets of *Orsonwelles polites* (Fig. 62) and *O. malus* Hormiga, 2002 (Fig. 61D, lower left), and Australian genus 1 sp. GH01 (in which the short runway was expanded slightly at its tip) (Figs. 15C–E). Some runways were difficult to distinguish from tubes (above).

Perforated Sheets. Nearly all sheets were continuous, without any objects such as a twig passing through them or through their tangles. In a few, an object such as a twig penetrated or passed through the sheet. *Microlinyphia dana* (Fig. 49I) and *Juanferandezia melanocephala* (Figs. 29A–C) had a small open space in the sheet around the object. In contrast, the sheet of *Tapinopa bilineata* (Figs. 76E, F) had no openings. Given that these objects all appeared to be rigid and probably immobile, the open spaces may have resulted from the spider’s

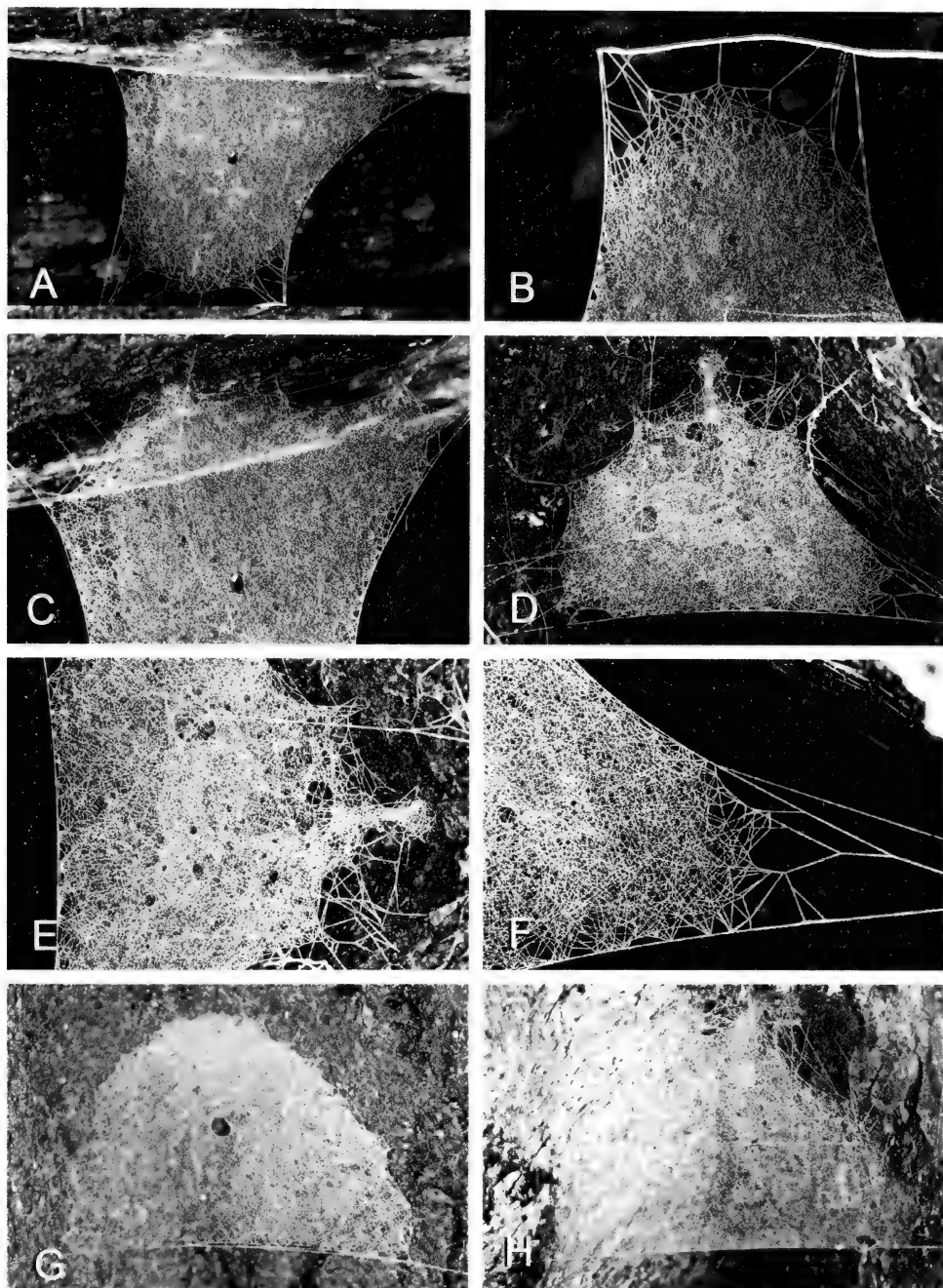


Figure 15. Australian genus 1 webs (1). (A–C) Australian genus 1 GH01, female. Australia. New South Wales, Dorrig National Park (DSC_2776.NEF, DSC_2779.NEF, DSC_2780.NEF). (D–F) Australian genus 1 GH01, female. Australia, New South Wales, Dorrig National Park (DSC_2794.NEF, DSC_2796.NEF, DSC_2801.NEF). (G, H) Australian genus 1 GH01, female. Australia, Queensland, Tamborine National Park (GH020417_R04_31_AUS_Laetesia.tif, GH020417_R04_36_AUS_Laetesia.tif).

construction behavior, rather than from damage to the sheet produced by movements of the object. The holes around penetrating objects in the sheets of two other linyphiids, *Neriere coosa* and *Neriere litigiosa*, may have been caused by movements of the flexible plant structures that frequently penetrated sheets (Eberhard, 2022; W. Eberhard, unpublished).

Central Hub-like Areas. Another study described hub-like areas in the central, uppermost portions of the domes in *Diplothyron simplicatus* (F. O. Pickard-Cambridge, 1902) and *Neriere coosa*, where the spider rested (Eberhard, 2022). The areas usually had one or more holes, and the lines seemed to be less dense and shorter (Eberhard, 2022), giving the impression that the spider may have removed and then replaced lines. It was not possible, however, to follow individual lines reliably, even in sheets built in captivity, so this impression could not be quantified. Similar apparently modified areas occurred in *Florinda coccinea* (Hentz, 1850) sheets built in captivity (W. Eberhard, unpublished).

Similar hub-like modifications were seldom clear in this study. One possible example is Australian genus 1 sp. GH05 (Fig. 17D); less certain cases occurred in the sheets of *Dubiaranea insulana* (Fig. 23D, at the peak of the largest dimple), *Laetesia* sp. GHG02 (Figs. 35A, E, in the middle near the top of the dome), and close to the very center of the sheet of both *Australolinyphia remota* (Fig. 19G) and Australian genus 2 sp. GH01 (Fig. 14E). One possible explanation for this difference is that most of the closeup photos of sheets in this study were not of the central area but rather the edges, where tangle lines did not obscure the sheet. Other possible observational difficulties resulted from apparent raindrop damage, as in *Laminacauda propinqua* (Fig. 39C), repairs of damage to sheets (above), and dense tangle lines that obscured the sheet structure. Nonetheless, it was clear that the central area was not

modified in some clear photos of apparently intact, naked sheets in Australian genus 1 sp. GH03 (Figs. 17A, B), *Laminacauda* sp. “chdes” (Fig. 38F), and (probably) *Dubiaranea* sp. Ecuador (Fig. 25C). In general, it is uncertain whether the species in this study had similar hubs.

Another possible reason for a lack of a modified central area would be if the spider rests at the edge of the web rather than in the center. Thus, *Diplothyron diana*e (Fig. 20B), *Labulla thoracica* (Figs. 31B, F), and *Himalaphantes* sp. (Fig. 28E) all apparently lacked a modified central area, and their sheets were especially dense at one protected edge where it abutted against the substrate (Figs. 20A, upper edge; 31B and 28E, upper right; 31F, middle right). Further observations will be needed to determine the frequency of hub-like areas and test the hypothesis that they are associated with the spider’s resting site.

Sticky Lines. We can only comment briefly on the presence of sticky lines because they could not be distinguished from nonsticky lines when coated with powder. Many lines in the sheet of *Dubiaranea lugubris* bore droplets so large that they were easily distinguished with the naked eye (Figs. 22C, D). Smaller droplets that are difficult or impossible to distinguish with the naked eye are known in both the sheets and the tangles of several other linyphiid species (summary in Eberhard, 2021) and may well have been present in some (or even all) of the species illustrated here. An estimated 50% of lines in the sheet and at least some lines in the upper tangle of a web of a *Frontinella pyramitela* web built in captivity bore small droplets, and the majority of lines in the sheet and at least some of those in the upper tangle in a *Florinda coccinea* web built in captivity and in the sheet of *Neriere litigiosa* also bore droplets (W. Eberhard, unpublished). The Brazilian species *Pocobletus riberoi* (Lemos & Brescovit, 2013) builds a sheet web with an upper and lower tangle; lines in at least

the upper tangle were sticky, even after it was lightly dusted with cornstarch (as assessed by light contact with the blunt metal end of a mechanical pencil in three different webs).

The triad of spigots on the posterior lateral spinnerets, which is known in araneoid spiders to produce lines coated with droplets of sticky liquid, is present in almost all linyphiids that have been examined (e.g., Horniga, 1994b, 2000), including the genera whose webs are illustrated here, and droplets on lines have been observed directly in others (summarized in Eberhard, 2021). The presence of triads in many of the species of genera whose webs are illustrated here, including *Agyneta*, *Diplothyron*, *Frontinella*, *Laminacauda*, *Lepthyphantes*, *Linyphia*, *Microlinyphia*, *Neriere*, *Orsonwelles*, *Ostearius*, and *Walckenaeria*, implies that many of these webs had sticky lines. Tiny droplets of liquid also occur in the webs of some theridiids, such as *Anelosimus* spp. and *Tidarren sisypoides* (Walckenaer, 1841) (Madrigal-Brenes and Barrantes, 2009).

Tangles

A “tangle” was defined as a three-dimensional network with no perceptible organization. Because of the large intraspecific variation in the outlines of the tangles above and below sheets (e.g., Figs. 58, 78, 79A, B; also Eberhard, 2022), we did not include the forms of the outlines of tangles (triangular, etc.) in our analyses. The tangle above the main sheet was termed the upper tangle; one below the main sheet was the lower tangle. (These tangles have also been called the upper and lower scaffolding; Arnedo et al., 2009). It is worth noting that linyphiids and pimoids always moved under their sheets (except for brief forays to attack prey in the upper tangle), which means that the lines above the sheet (and also most if not all of those below the sheet) were presumably the result of building behavior

and not incidental drag lines left behind as the spider moved about its web.

Upper Tangles. Upper tangles took many forms. Tall upper tangles were more than a sheet diameter tall, as in *Acroterius* spp. (Figs. 78, 79B), *Pocobletus* sp. GH02 (Fig. 74C), *Diplothyron* sp. (Fig. 20D), and *Novafrontina uncata* (F. O. Pickard-Cambridge, 1902) (Fig. 58A). Tall upper tangles such as those of *Pocobletus* sp. Dominican Republic were consistently dense (Fig. 68B) or relatively dense (Fig. 68C). At the other extreme were low upper tangles, which were usually sparse, as in *Laetesia raveni* (Fig. 33B), but sometimes dense, as in *Novafrontina uncata* (Fig. 58H). Some sparse upper tangles were restricted to locations just above the site near the edge of the web where the spider apparently rested, as in *Agyneta* spp. (Figs. 11C, D, 12A, B) and *Dubiaranea* sp. Ecuador (Fig. 25B). (This spider rested off the web during the day but in the center at night.) Some other apparent retreats lacked tangles, however, as in *Agyneta* sp. (Figs. 11A, B, E–H). One such tangle contained two white egg sacs (Fig. 11D). (In contrast with Theridiidae, linyphiid egg sacs are seldom associated with webs; e.g., Nielsen, 1932.) Upper tangles never included sheet-like structures like those in some lower tangles (below).

In general, lines in the upper tangle did not have discernible patterns, but a few upper tangles were largely composed of long straight, approximately vertical lines, as in *Acroterius* sp. (Fig. 78) and *Dubiaranea* sp. Ecuador (Fig. 23G).

Lower Tangles. Lower tangles were usually less dense than upper tangles, although Australian genus 3 sp. GH02 (Fig. 18F) and *Laminacauda* sp. “fCh” (Fig. 43E) were exceptions. Some lower tangles included sheets (see “double sheets” above), but the distinction between lower sheets and tangles was sometimes difficult; some sheets were so sparse (e.g., Figs. 55G, H of *Neriere helsdingeni*) that it

was not easy to distinguish them from small tangles. The sizes, locations, and forms of lower sheets varied. The dense lower tangle of one web of Australian genus 3 sp. GH02 lacked a second sheet but had a curved upper margin that was parallel to and just below the principal sheet (Fig. 18F). Some cup-shaped sheets had a centered lower tangle that was limited to the space directly below the lowest portion of the cup (where spiders generally rested), as in *Laminacauda* sp. "fCh" (Figs. 43D, E). When the sheet of *Agyneta semipallida* (Chamberlin & Ivie, 1944) (Figs. 11E, F) was carefully peeled away, a sparse tangle was revealed below. In some photos it was not possible to check for lines directly below the sheet, so similar inconspicuous tangles may have occurred but been missed in some webs (e.g., other *Agyneta* species).

Combinations of Sheet and Tangle Traits

There were many combinations of the different sheet and tangle traits. To cite just a single example, the web of *Pocobletus* sp. Dominican Republic (Figs. 68C, D) was an elevated, moderately cup-shaped, dense unobstructed sheet with long frame lines; a wide, tall, dense upper tangle; and a less dense, narrow lower tangle that was centered under the lower portion of the cup. Many different combinations are noted in the discussions below. Further work will be needed to determine whether, as seems likely, some taxa are characterized by particular combinations of these web traits.

Cyatholipidae

As noted in the introduction, Cyatholipidae appears to be the family most closely related to linyphioids. The webs of one species in each of five cyatholipid genera are illustrated in Figures 3–7. These webs share several traits seen in linyphioid webs. They all have elevated, nearly horizontal, flat or nearly flat, unobstructed, and densely meshed sheets that lack dimples. Apparent

repairs of holes were visible in the sheets of *Forstera* sp. (Figs. 3A, B, D–F) and *Wanzia* sp. (Figs. 7E–G). The density of lines was reduced near the edge of the sheet in *Forstera* sp. (Figs. 3D, F, 6D). Frame lines with "V" attachments and scattered cases of parallel lines were clear in areas of one web of *Forstera* sp. (Fig. 3) where density was lower.

One difference with nearly all linyphioid webs was the following combination of traits: *Forstera* sp., *Matilda* sp., *Ulwembua* sp., and one web of *Wanzia* were nearly (Fig. 5A) or entirely naked (Figs. 3A, B, D, 4A, B, 6A–D, 7A) and were also (except for *Matilda* sp.) substantially elevated above the ground. *Teemenaarus* sp., however, had a tangle above and below the sheet, with an open space just below the sheet (Fig. 4D), as in linyphioids. *Tekelloides* sp. differs from all known linyphioids in that the spider rests on lines in the sparse tangle below its dense sheet rather than on the sheet itself (Forster and Forster, 2005). One web of *Wanzia fako* Griswold, 1998, had a nearly planar tangle below one side of the sheet (Figs. 7B, C) (perhaps below the spider's resting site?) but none above. Although we do not have quantitative data, in many cases the sheet seemed to be larger relative to the spider's size than is typical for linyphioids (e.g., in Fig. 4A the spider is minute relative to the size of the sheet). Cyatholipids generally rested near the central portion of the sheet.

Physoglenidae

As noted in the introduction, physoglenids may be closely related to the group linyphioids + Cyatholipidae. The webs of one species in each of seven genera are illustrated in Figures 8–10. Physoglenid webs shared several traits with those of cyatholipids and linyphioids. All webs included an elevated, approximately horizontal sheet that was sparse to moderately dense. In all cases in which it was possible to judge, the sheet was at least weakly

domed. The spiders rested at the peaks of these domed sheets (Figs. 8A, D). The sheet of *Pahora* sp. had a tangle above and below (Fig. 8E).

There were also several differences. All physoglenid sheets were less dense than all cyatholipid sheets. They also differed from cyatholipids in lacking clear “V” attachments to the frame lines. The webs of *Chileotaxus sans* Platnick, 1990, differed from all linyphioids and cyatholipids in forming a sharply curved dome that extended in places into a large nearly horizontal sheet with a very low, sparse upper tangle (Figs. 8A, B). The top of one such dome was just under a plant leaf (Fig. 8B); these web traits are very similar to those of the pholcid *Modisimus bribri* Huber, 1998 (Eberhard, 2020). The sheets of *Mangua medialis* Forster, 1990, and *Pahora* sp. were also domed but had taller tangles above the sheet (Figs. 8D, E), as did the less sharply domed sheet of *Paratupua* sp. (Fig. 9E). In *Physoglenes puyehue* Platnick, 1990 (Figs. 9A, B), and *Paratupua* sp. (Fig. 9D) the upper tangles were sparse and limited to only the higher portions of the weakly domed sheets.

DISCUSSION

Diversity of Web Forms

Nearly all of the species in this study built sheets, and nearly all of these sheets were continuous and more or less horizontal. Thus, to a first approximation, this survey confirms the view that linyphioid webs are relatively uniform. The sheets and the lines accompanying them varied, however, in many respects, including the following: presence and relative size and density of tangles above or below the sheet; placement, especially close to the substrate, whose contours define the contour of the web (defined as “substrate webs” in Hormiga [2007] and Arnedo et al. [2009]); densities and several geometric patterns of lines in the sheet; coatings of “slime” or

sticky droplets on lines in the sheet; the presence of a runway (that is sometimes tube- or funnel-like) from a more sheltered site to the sheet; the degree of definition of the plane itself; the presence of downward- or upward-projecting dimples in the sheet; the presence of a cylindrical retreat at one edge of the sheet; curves in both the main sheet and lower sheets (cup-shaped, dome-shaped, flat, etc.); perforation of the sheet by objects like twigs and leaves; and the presence of additional sheets and their relative sizes and densities.

Even though current knowledge of linyphiid webs is still only fragmentary, it is clear that the label “sheet web” has hidden a great deal of diversity. This diversity in linyphiid webs resembles, although at a smaller scale, the same pattern of diversity seen in spider webs in general, and in sheet webs in particular (Eberhard, 2020). Previous statements to the effect that linyphiid webs lack diversity are thus only partially correct. Linyphiid webs do indeed usually include sheets, but they have many variations on this basic design. The term “sheet web” has thus been something of a linguistic trap that has hidden many different designs under a single name. For further discussions of problems associated with the term “sheet,” see Peters and Kooor (1991), Blackledge et al. (2009, supplementary materials), Eberhard and Hazzi (2017), and Eberhard (2020).

It is worth noting, however, that this variation may have limitations: no known webs with a dome-shaped principal sheet have a second sheet; flat sheets near the ground nearly always have little or no upper tangle; in cases of intraspecific variation in the presence of a sheet, the lower sheet, but never the principal sheet, is sometimes reduced to only a tangle; in only a single species (*Tekelloides* sp., a cyatholipid rather than a linyphioid) does the spider rest in a tangle below a sheet rather than on the sheet itself; to the best of our knowledge,

the same species never builds both cup- and dome-shaped sheets.

Intragenetic Similarities and Differences

If one assumes that the species that are presently grouped in genera are each other's closest relatives (i.e., the genera are monophyletic), data are now sufficient to begin searching for patterns in web evolution by checking for similarities and differences within genera. Although phylogenetic analyses have tested the monophyly of some of the genera treated here, such as *Orsonvelles* (Hormiga et al., 2003), *Laminacauda* (Arnedo and Hormiga, 2021), and *Diplothyron* (Silva-Moreira and Hormiga, 2022), most linyphiid genera have not received a phylogenetic treatment. We discuss below the genera in which the webs of more than a single species have been documented, in decreasing order of the apparent intragenetic diversity, and of the sample size by genus. We include information from other publications with web photographs and mention the sample size for each species and the fraction of species in the genus whose webs are known to emphasize the limits of current knowledge. (Webs are known in only two or three species in 14 of the 21 genera.) Both species and genera can be expected to display greater ranges of diversity when larger samples become available (see the section on intraspecific variation below).

Linyphiidae

High Intragenetic Diversity. LAMINACAUDA (WEBS OF 11–12 SPECIES). The erigonine genus *Laminacauda* comprises 40 species, mainly from South America, but new species remain to be described (G. Hormiga, unpublished). Some of the undescribed species are included in our sample, which is largely composed of species endemic to the south Pacific archipelago of Juan Fernandez. The 11–12 species of *Laminacauda* (Figs. 36–44) show the greatest intragenetic

diversity yet documented in a linyphiid genus. The diversity of species and webs in Juan Fernandez is most likely the result of an adaptive radiation in depauperate environments (Arnedo and Hormiga, 2021). Most sheets were medium to sparsely meshed and highly elevated with moderately sparse tangles, but with exceptions (below), and they showed many other differences that were so striking that nearly every species (and even some different conspecific individuals) exhibited distinctive variations in design, to the extent that some of the species in Juan Fernandez could be identified by just examining their webs. The upper end of the domed sheet extended into a tube in some *L. ansoni* (Figs. 36A, D, E); in one of these webs (but not the others) the tube reached the substrate (the trunk of a tree), and often these silk tubes led to retreats in circular openings on tree trunks made by xylophagous insects. No sheet was discernible, however, in another *L. ansoni* web (Fig. 36C), and the sheet of still another individual of the same species appeared to be roughly cup-shaped (Fig. 36B).

The sheets of *L. malkini* were flat, relatively small, and sparse, with very sparse upper tangles. One sheet formed a tube at one edge (Fig. 37C), whereas others lacked even a hint of a tube (Figs. 37E, F). The sheets of *L. rubens* (Figs. 38A–E) were unique in being vertical and very close (on the order of the length of a spider or less) to the trunk of a tree. The upper edge of some sheets was curved to form a tube in which the spider rested (Figs. 38B, C), but others lacked a clear tube (Fig. 38A). A tangle “above” the sheet varied greatly in its extension (compare Fig. 38A with Fig. 38D). In addition to the data provided by the webs photographed, the webs of many other individuals of *L. ansoni* and *L. rubens* were examined, because both species are relatively common in the native forests of Robinson Crusoe Island. The sheet of *Laminacauda* “chdes” (also from Robinson

Crusoe Island) had a different, ridge tent-like form just above the leaf litter; an uppermost central ridge slanted upward toward a large leaf with no discernible tangle lines (Fig. 38F). The web of *L. tuberosa* was, in contrast, unremarkable, with a dense weakly cupped sheet that sloped slightly upward at some edges, with a very sparse upper tangle and moderate lower tangle (Fig. 39H). The webs of *L. propinqua* (a species endemic to Alejandro Selkirk Island) were weakly domed sheets near the leaf litter whose mesh varied from dense (Fig. 39C) to only moderate (Figs. 39D, F). Upper tangles were absent or only sparse above. One sheet had plant stems projecting through it (Fig. 39B).

All six webs of *Laminacauda magna* (another Robinson Crusoe endemic) had a naked or nearly naked, medium-meshed, bumpy horizontal sheet near the ground (Figs. 40–42). Two of these sheets had small glistening patches (Figs. 40B, 42A, B) that were not perceptibly sticky, but similar patches were absent in other webs of this species. A horizontal view of one web revealed that it was a “sandwich,” with a second, less densely meshed horizontal sheet immediately below the principal sheet (Fig. 41D). It was difficult to distinguish the presence of the lower sheet in a vertical view of this same web from above (Fig. 41C), leading us to question whether some or all of the other webs of this species (all seen from above) may have also had second lower sheets. This possibility of a second sheet seemed unlikely, however, in some especially clear photos (Figs. 40A, 42A).

One web in each of two other Robinson Crusoe species, *Laminacauda* sp. “fPC” and *Laminacauda* sp. “fCh” (Fig. 43), resembled those in some other genera outside the subfamily Erigoninae, with highly elevated, dense, moderately cup-shaped sheets with multiple dimples; a very sparse upper tangle; and a moderately dense lower tangle. In *Laminacauda* sp. “fPC” the lower tangle was as wide as the

sheet, whereas in *Laminacauda* “fCh” the lower tangle was limited to the central portion of the sheet under the lowest portion of the cup.

In some senses, the most distinct web was that of the continental species *L. parvipalpis*, whose five webs were all near the ground. Three webs (Figs. 44B, C, E) appeared to be more or less horizontal sheets, whose sparse mesh became gradually more dense near one edge, giving the impression that there was a retreat under the adjoining leaf litter (there is an upper tangle in Fig. 44B, little if any above Fig. 44C, and none in Fig. 44E). This sheet design differed from all other known linyphiid webs. One other web (Fig. 44D) was a loose tangle in which we could not discern any organization (perhaps because it was in the early stages of web construction); the other web was even more difficult to describe (Fig. 44A).

One web of a *Laminacauda newtoni* Millidge, 1985, from continental Chile (Miller, 2007: fig. 1A) also suggested a sparsely meshed, perhaps naked sheet near the substrate whose more sheltered side abutted on the substrate and was somewhat more densely meshed, but details could not be resolved confidently. The web of an additional *Laminacauda* sp., also from continental Chile (Miller, 2007: figs. 1B, C), was near the substrate, but the photo was not clear enough to resolve details other than long lines in what appeared to be an upper tangle. The simple, somewhat irregular webs of these three continental species are representative of the webs of other continental species and of other South American erigonines that live in the leaf litter or among rocks and possibly represent the plesiomorphic web architecture of *Laminacauda*.

In sum, the webs of *Laminacauda* species differed in many respects, including web site (near leaf litter, highly elevated), sheet mesh (sparse, dense, asymmetrically dense near one edge, shiny patches), sheet

form (cup, dome, flat, curled to form lateral tube, tube-shaped extension of top of dome, sandwich), and sheet orientation (horizontal, vertical).

NERIENE (WEBS OF NINE SPECIES HERE PLUS SEVEN IN PREVIOUS PUBLICATIONS)

The genus *Nerienne* includes about 60 described species, mostly in Eurasia and Africa. The webs of nine species of *Nerienne* illustrated here (from Taiwan, the United States, Cameroon, and Thailand) were uniform in all being highly elevated, with relatively densely meshed sheets. One group had tall, relatively dense upper tangles. Where visible, the lower tangle was relatively sparse, and it may have been absent in some webs. The forms of the sheets varied dramatically. The most unusual was the uniquely asymmetrical cup-shaped sheet of *Nerienne* sp. GH03 (Figs. 52A–E) from Taiwan, in which one side of the cup was much larger than the others and formed a vertical wall on one side of the web (Figs. 52A–C); a second web of this species had a similar, although less pronounced asymmetry (Figs. 52D, E). The sheet of a second species, *Nerienne* sp. GH01 (from Taiwan as well) also had one side that was much higher than the others, but it was flat rather than cupped and had a relatively smaller upper tangle (Fig. 50F). The sheets of single webs of the Asian species *N.* (= *Neoliniphia*) *fusca* (Oi, 1960) and *N.* (= *Neoliniphia*) *angulifera* (Schenkel, 1953) were also deeply cupped; the cup of *N. japonica* (Oi, 1960) was even deeper (Shinkai and Takano, 1984). The cup was symmetrical in at least the last two species (Shinkai and Takano, 1984).

The sheets of three other *Nerienne* species, the North American *N. litigiosa* (Figs. 53G, 56; also Comstock, 1967), the Holarctic *N. radiata* (= *marginata*) (Emerton, 1902; Comstock, 1967), and the Asian *N.* (= *Proliniphia*) *longipedella* (Bösenberg & Strand, 1906) (Shinkai and Takano, 1984)

contrasted sharply: they were all relatively symmetrical and strongly domed rather than cupped. (They resembled almost perfect upside down versions of the sheet of *N. japonica*.) The sheets of three *N. albolimbata* (Figs. 50A–E) from Asia and the Palearctic *N.* (= *Proliniphia*) *emphana* (Walckenaer, 1841) (Shinkai and Takano, 1984) had less extremely pronounced domes and lower upper tangles; the upper tip of the dome was especially sharp in one *N. albolimbata* web (Figs. 50A, B). Still other *Nerienne* species with tall upper tangles had intermediate sheet forms. The sheets of four *N. oxycera* webs (from Thailand) varied: two were weakly cupped (Figs. 54A, B), one with an especially dense lower tangle (Fig. 54A); one was nearly flat (Fig. 54C); and one was weakly domed (Figs. 54D, E). The domed sheet had fewer downward-directed dimples. The shapes of five sheets of *N. helsdingeni* (from Cameroon) varied between weakly domed (Fig. 55H), flat (Figs. 55F, G), and weakly saddle-shaped (Figs. 55A, C, D).

The upper tangles were not as tall and less dense in several other *Nerienne* species. In two webs of the North American *N. digna* the sheet was nearly flat but slightly cup-shaped in form, with a small area of dense lower tangle below the bottom of the cup (Figs. 50G, H). One of these webs had a well-developed upper tangle covering most of the web (Fig. 50G), but the upper tangle in the other was sparse and not tall and was limited to near the area covered by the lower tangle (Fig. 50H). Three webs of *N. clathrata* (Fig. 51) were similar to those of *N. digna*. Their flat to slightly cup-shaped sheets were especially dense, and at least two of them had downward-directed dimples (Figs. 51A, B, H). All three webs were built against the bases of standing tree trunks. Their upper tangles ranged from sparse (Figs. 51D–F) to moderate (Figs. 51A, G). A fragment of a former sheet may have been below one web with little lower tangle (Fig. 51H). The web of *Nerienne* sp.

GH01 from Taiwan had an even less extensive upper tangle that was concentrated in the area above the small lower tangle; both were associated with the bottom of the cup, which was presumably where the spider rested. This sheet differed in being more clearly cup-shaped (Fig. 50F). Still another combination with a small upper tangle occurs in the North American *N. coosa*, in which the sheet was weakly domed rather than cup-shaped, and both upper and lower tangles were reduced and more or less limited to the area of the web where the spider rests; these webs were built close to but not against the ground (Eberhard 2021, 2022).

The three webs of the North American *N. variabilis* (Figs. 53C–F) differed in that the dense sheet was very near the ground and close to large objects (the bases of tree trunks); the sheet was flat or very weakly domed, but with numerous small upward-projecting dimples. These webs had moderately dense upper tangles but, because of the short distance between the sheet and the ground, probably lacked lower tangles. The web of *Neriene* sp. GH02 from Taiwan was quite similar, with a perhaps less densely meshed sheet that appeared to slant upward toward the tree trunk (Figs. 53A, B).

In summary, sheets of *Neriene* species ranged from deeply cupped to sharply domed, with multiple intermediates; most sheets were highly elevated but were just above the ground in one species. The upper tangles ranged from tall and dense to sparse, with lower tangles from absent to dense just below the bottom of the sheet cup.

TAPINOPA (WEBS OF THREE SPECIES)

The genus *Tapinopa* includes eight described species from the Holarctic region and Southeast Asia. The web of the Palearctic species *Tapinopa longidens* was a flat sheet covered with slime in the leaf litter and lacking apparent tangles (Fig. 76A), as has been documented previously

(Nielsen, 1932; Bristowe, 1941). The webs of other *Tapinopa* species were dramatically different. The highly elevated webs of the Nearctic *T. bilineata* consisted of a pair of flat horizontal sheets (a “sandwich”) with very long frame lines projecting from the surface of a vertical tree trunk, with few if any tangle lines (Figs. 76E, F); they had no slimy material. The enclosed nature of these webs vaguely resembled the “purse” webs of atypid mygalomorphs (*Atypus* and *Sphodros*) and the aberrant araneid *Paraplectanoides crassipes* Keyserling, 1886 (Hickman, 1975; Eberhard, 2020). One *T. bilineata* web had a thick stick protruding through both sheets (Figs. 76E, F). Two webs of *Tapinopa vara* Locket, 1982, the only *Tapinopa* species found in Southeast Asia, were still different. One had a moderately densely meshed dome-shaped sheet, with a moderately dense tangle above (Fig. 76C); the other may have been a sparsely meshed dome with moderate tangle above, but the photo was difficult to interpret (Fig. 76B). Both of these webs were built on the forest floor; neither web of *T. vara* had a coating of slime.

ACROTERIUS (WEBS OF TWO SPECIES)

The recently erected genus *Acroterius* includes a dozen described species from China, but an unknown number of yet to be named species exist, including the two species from Taiwan and northern Thailand whose webs are illustrated here. The webs of these two species differ dramatically. The web of *Acroterius* sp. Thailand (Figs. 65F, G) had a weakly domed, only moderately densely meshed sheet, a moderate tangle above, and perhaps little or no tangle below. The sheet was pulled upward in numerous small dimples (Fig. 65G). In contrast, nine webs of *Acroterius* sp. GH01 (from Taiwan) (Figs. 78, 79) had a dense sheet whose form ranged from sharply cupped to nearly flat (Fig. 79F). All of the sheets had multiple downward-directed dimples. Seven of these webs had a second, less dense, and smaller diameter cup-shaped sheet immediately

below the larger sheet, although in some cases it was strongly reduced (Fig. 78); the second sheet was apparently lacking, however, in the other two webs, which had only a sparse tangle below the sheet (Figs. 79E, F). All webs had an upper tangle but its height varied. In one case it extended more than two sheet diameters above (Fig. 78); in other webs it was smaller (Figs. 79A–C). The density of the upper tangle ranged from dense (Figs. 78, 79B) to sparse (Fig. 79E). None of the Taiwan webs was dome-shaped.

Moderate Intrageneric Diversity. AGYNETA (WEBS OF 12 SPECIES). *Agyneta* is a large genus with about two hundred described species and a world distribution; many undescribed species are presumed to exist. Twelve species of *Agyneta* showed a mix of consistency and variation in their webs. All webs were naked or nearly naked planar sheets near the ground. The sheets of perhaps eight species had the otherwise unique pattern of many lines radiating from one corner of the sheet, which appeared to have a small tangle retreat (Figs. 11–13). In three of these species a small tangle was immediately above the retreat (Figs. 11C, D, 13A–C). Three other species, however, had similar naked planar sheets near the ground but lacked the converging lines (Figs. 12G, H, 13E, F), and one (Fig. 13D) was more elevated. A 12th species differed strikingly (Figs. 12D–F). It had a unique trough-like sheet built close to the upper surface of a curled leaf in the ground litter, with an extensive upper tangle that spanned the leaf's curl and a much smaller lower sheet. *POCOBLETUS* (WEBS OF 10?) SPECIES, ALL BUT ONE UNDESCRIBED)

The American genus *Pocobletus* groups 13 described species, mostly from the Neotropical region, but many others remain to be described (G. Hormiga, unpublished). Six webs of *Pocobletus* sp. GH32 from Brazil (Figs. 66 A–F, 67A, B) had highly elevated, flat or very weakly cupped dense sheets with few or no dimples. They were

unusual in having lower tangles that were more extensive than the upper tangles; one web lacked an upper tangle altogether (Fig. 66C). Four of the lower tangles were more or less limited to the central, lowest area of the sheet, presumably where the spider rested. Five webs of *Pocobletus* sp. GH33 from the Dominican Republic were similar in having highly elevated dense sheets and moderately dense lower tangles limited to the central portion of the sheet. They differed from the Brazilian species in having clearly cup-shaped sheets with downward-projecting dimples (especially in the central area in Fig. 68D), and in having moderately dense to dense upper tangles. Two webs of *Pocobletus* sp. GH02 from Costa Rica (Figs. 74C–F) were similar in having moderately to steeply sided cup-shaped sheets, with a few downward-directed dimples in the central portion. The lower tangles were denser in the central portion of the sheet but extended to the sheet's edges. In contrast, the lower tangle in one web of *Pocobletus* sp. GH05 from Colombia was limited to the central portion of the sheet, and there was little if any upper tangle. This web was similar to those just mentioned in having a highly elevated, dense, steeply sided, cup-shaped sheet (Fig. 72E).

Four of the five *Pocobletus* sp. GH01 from Panama (Figs. 68E, F, 69B–D, F) resembled the Brazilian species in having highly elevated, dense, flat (Fig. 69D) or weakly cup-shaped sheets that may have had fewer dimples than the Dominican Republic species (Fig. 68F) and dense, moderately tall upper tangles. They differed in having especially tall, dense, and wide lower tangles that were less strictly limited to only the central area of the sheet; in three, the lower tangle was as dense or denser than the upper tangle (Figs. 68E, F, 69B, D). The other web (Fig. 69A) was too battered to be useful.

Four of the five webs of *Pocobletus* sp. GH11 from Guyana (Figs. 70A–F, 71A)

also had highly elevated, dense, flat or weakly cup-shaped sheets with dense upper tangles, but they differed from all of the previous *Pocobletus* webs in that the lower tangle was a clear sheet (Figs. 70A–F, 71A). Three of four webs of *Pocobletus* sp. GH03 (Figs. 71F, G, 72A–D) also had sheet-like lower tangles that were just under the central portion of a highly elevated, dense, cup-shaped sheet. The slopes of the sides of the cup tended to be steeper than those of sp. GH11, varying from steep (Fig. 72E) to moderate (Fig. 72D) to weakly sloped (Fig. 72G). One web had numerous downward-directed dimples in the central two-thirds of the sheet (Fig. 72D). Four webs of still another species, *P. versicolor*, had clearly planar lower tangles (Figs. 72F, G, 73A–F). One of these webs was unique in having very long anchors that ran in only four different directions (Fig. 73E); the sheet of the lower tangle of this web was also unusual in being very close to the underside of the major sheet (Fig. 73F).

Three webs of *Pocobletus* sp. GH28 from Argentina (Figs. 71B–E), with dense, nearly flat sheets, differed from the others in being near the ground; three were next to tree trunks. They all had short upper tangles and a lower tangle that was sharply limited to the center of the sheet.

One web of *Pocobletus* sp. GH01 from Costa Rica (Figs. 74A, B) differed from the other *Pocobletus* species in being weakly domed rather than cupped; both the upper and lower tangles were limited to the central portion of the sheet. Although we do not have photographs, we observed multiple webs of *Pocobletus riberoi* at a single locality in the Atlantic forest in southern Brazil. Their webs, built on fallen trees and roots close to the forest floor, had upper and lower tangles and a horizontal, flat main sheet with downward-pointing dimples (pulled down by lines attached to the lower tangle). The upper and lower tangles were sometimes cone-shaped (with

the bases facing the sheet). At least some of the silk lines of the upper tangle were sticky.

In sum, the webs of *Pocobletus* generally had cup-shaped sheets with tangles above and below, but most species had at least one detail that set them apart from the webs of other congeners. Traits that varied included elevation above the substrate; the height, width, and density of the lower tangle; the height and density of the upper tangle; the form of the sheet; and the presence and location of dimples in the sheet.

AUSTRALIAN GENUS 1 (WEBS OF FIVE SPECIES)

This undescribed genus is from eastern Australia and Tasmania that putatively groups many as yet undescribed species. Seven webs of species GH01, three webs of GH03, two webs of GH05, and one web of GH06 were all elevated, naked, or nearly naked, approximately horizontal sheets with long frame or pseudo-frame lines that were located alongside vertical tree trunks; the sheets had low- to medium-density meshes that were more sparse near some edges. The two webs of GH02, in contrast, were just above the forest floor and had a sparse upper tangle above the central portion of the sheet. At least two of the GH01 sheets had a small, densely meshed “runway” extension on the sheltered side (Figs. 15C–E) that expanded slightly near the trunk, apparently forming a shelter for the spider that rested there during daytime. Similar extensions may have also been present in two other GH01 webs (Figs. 14B, 16A), but the photos were not clear on this point. Appropriate closeup photos were available to check for runways in two other species: the sheet of GH05 had a runway (Fig. 17E), but that of GH03 lacked a runway (Figs. 17A, C).

In sum, the webs of different species in this genus were similar in being more or less naked, relatively sparsely meshed sheets. The sheets differed, however, in the presence of short runways at the edge.

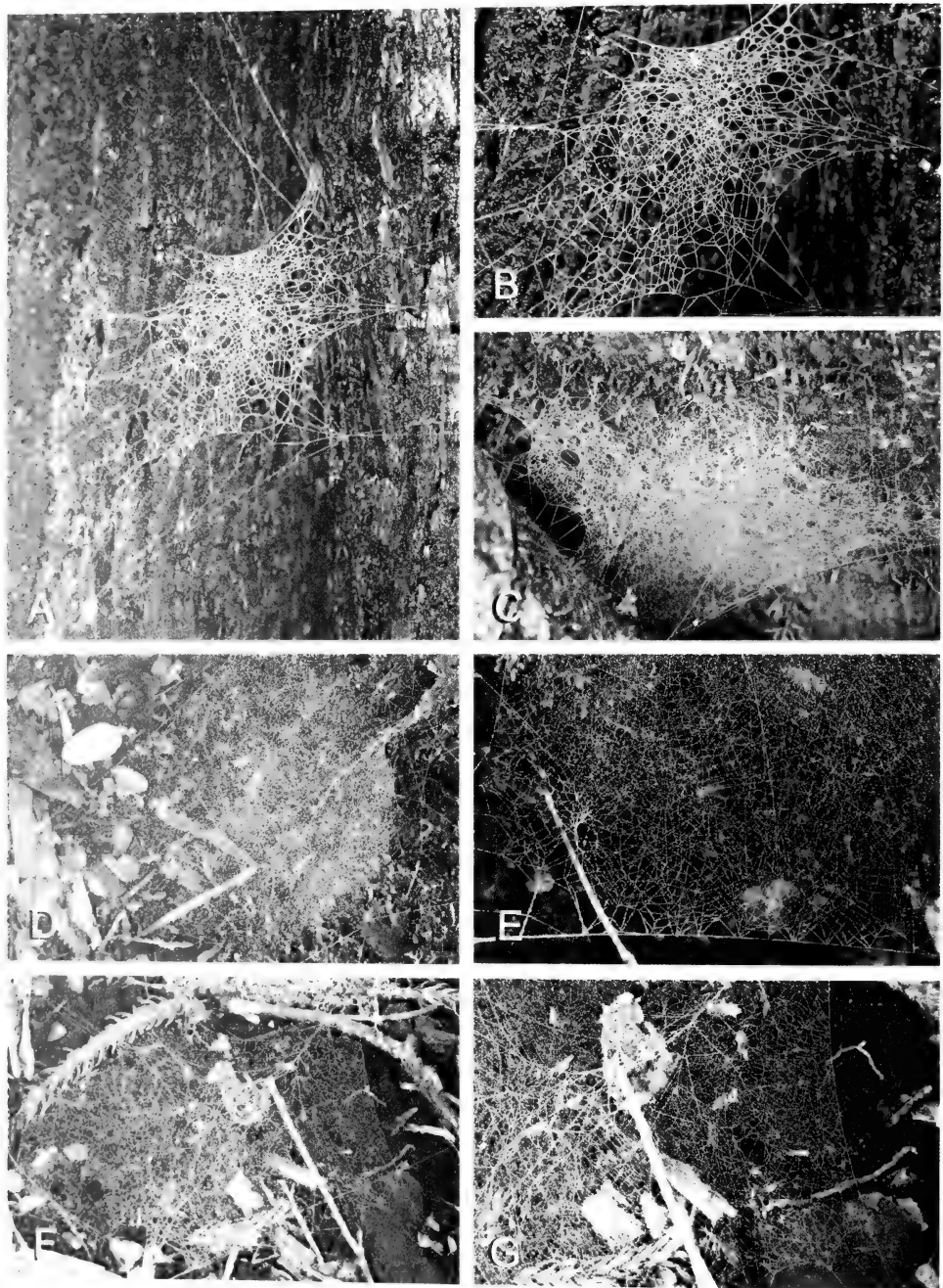


Figure 16. Australian genus 1 webs (2). (A, B) Australian genus 1 GH01, male and female. Australia (GH920718_R01_05_AUS_Laestesia.tif, GH920718_R01_10_AUS_Laestesia.tif). (C) Australian genus 1 GH01, female. Australia, Queensland, Lamington National Park (GH020414_R01_08_AUS_Laestesia.tif). (D, E) Australian genus 1 GH02, female. Australia, Tasmania, Franklin-Gordon Wild Rivers National Park (DSC_0506.NEF, DSC_0511.NEF). (F, G) Australian genus 1 GH02, female. Australia, Tasmania, Cradle Mountain National Park (DSC_0268.NEF, DSC_0270.NEF).

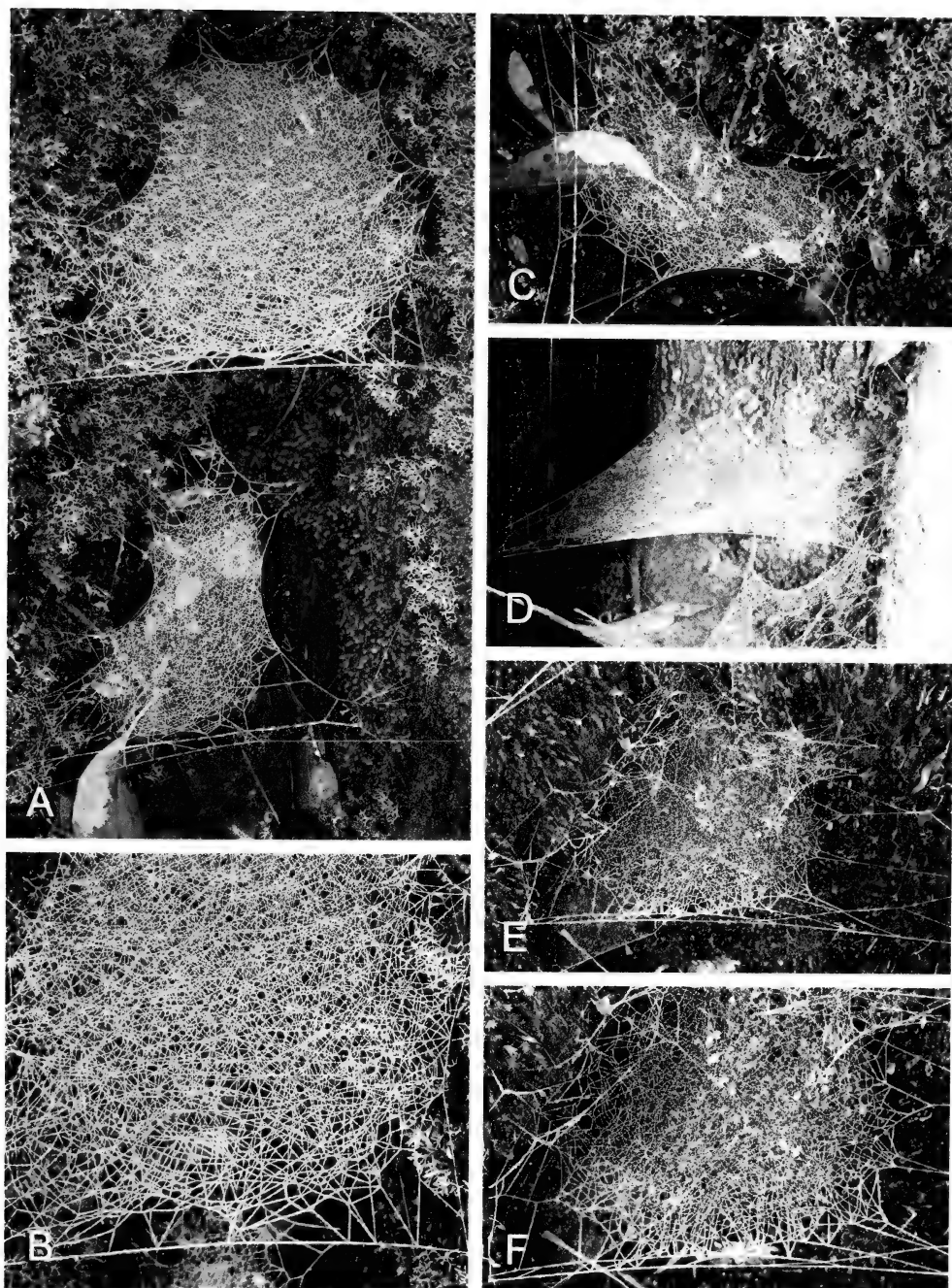


Figure 17. Australian genus 1 webs (3). (A, B) Australian genus 1 GH03, female. Australia, Victoria, Dandenong National Park (DSC_1495.NEF, DSC_1497.NEF). (C) Australian genus 1 GH03, female. Australia, Victoria, Dandenong National Park (DSC_1485.NEF). (D) Australian genus 1 GH05, female. Australia, Tasmania, Weldborough Pass Scenic Reserve (DSC_0362.NEF). (E, F) Australian genus 1 GH05, female. Australia, Tasmania, Mt. Field National Park (DSC_1592.NEF, DSC_1596.NEF).

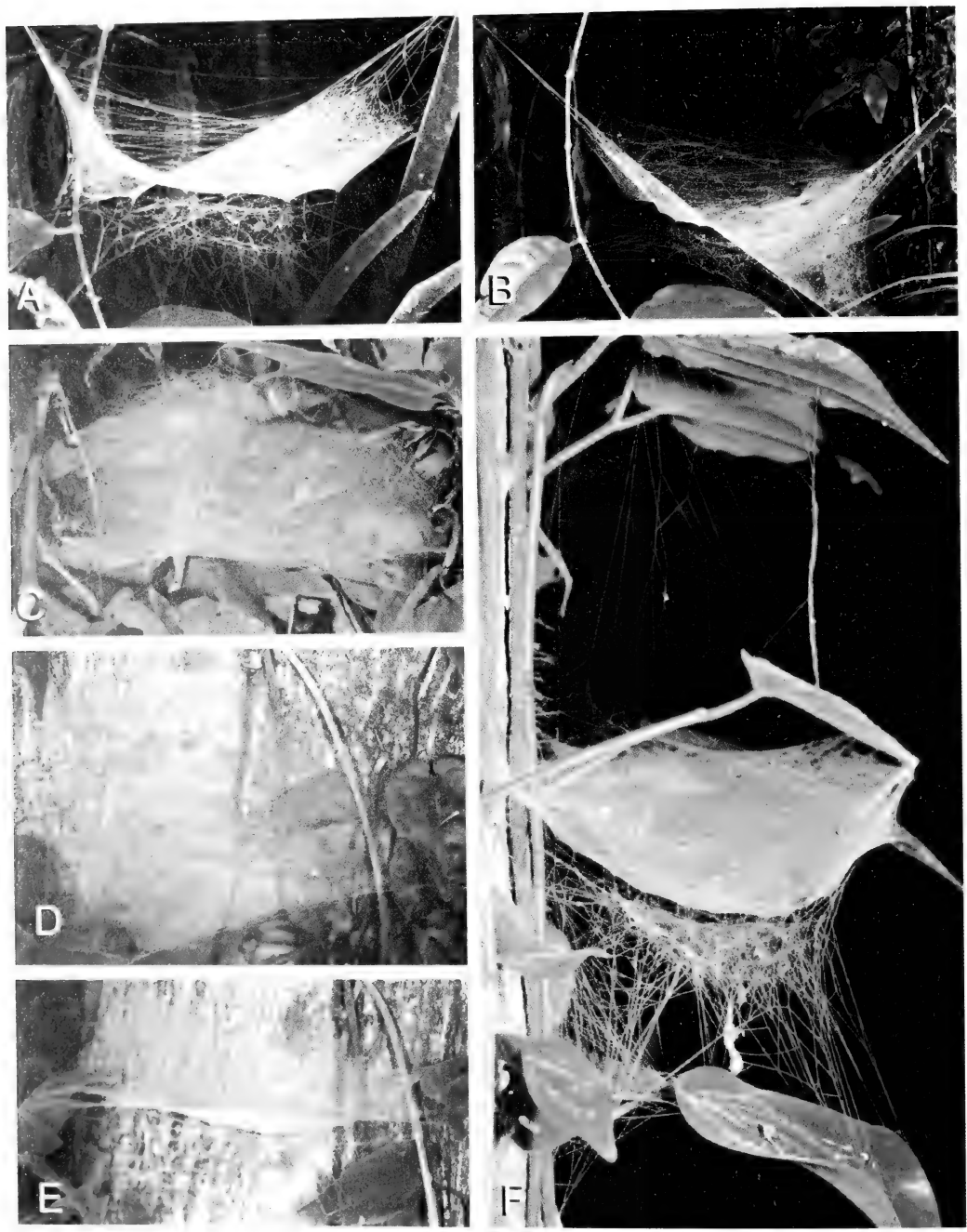


Figure 18. Australian genus 3 webs. (A, B) Australian genus 3 GH01, female. Australia, New South Wales, Dorrigo National Park (DSC_2817.NEF, DSC_2819.NEF). (C) Australian genus 3 GH01, female. Australia, Queensland, Lamington National Park, Binalong (GH020418_R06_08_AUS_ED.tif). (D, E) Australian genus 3 GH02, female. Australia, Queensland, Danbullia State Forest (GH020421_R09_03_AUS.tif, GH020421_R09_05_AUS.tif). (F) Australian genus 3 GH02, female. Australia, Queensland, Danbullia State Forest (GH020421_R09_11_AUS.tif).

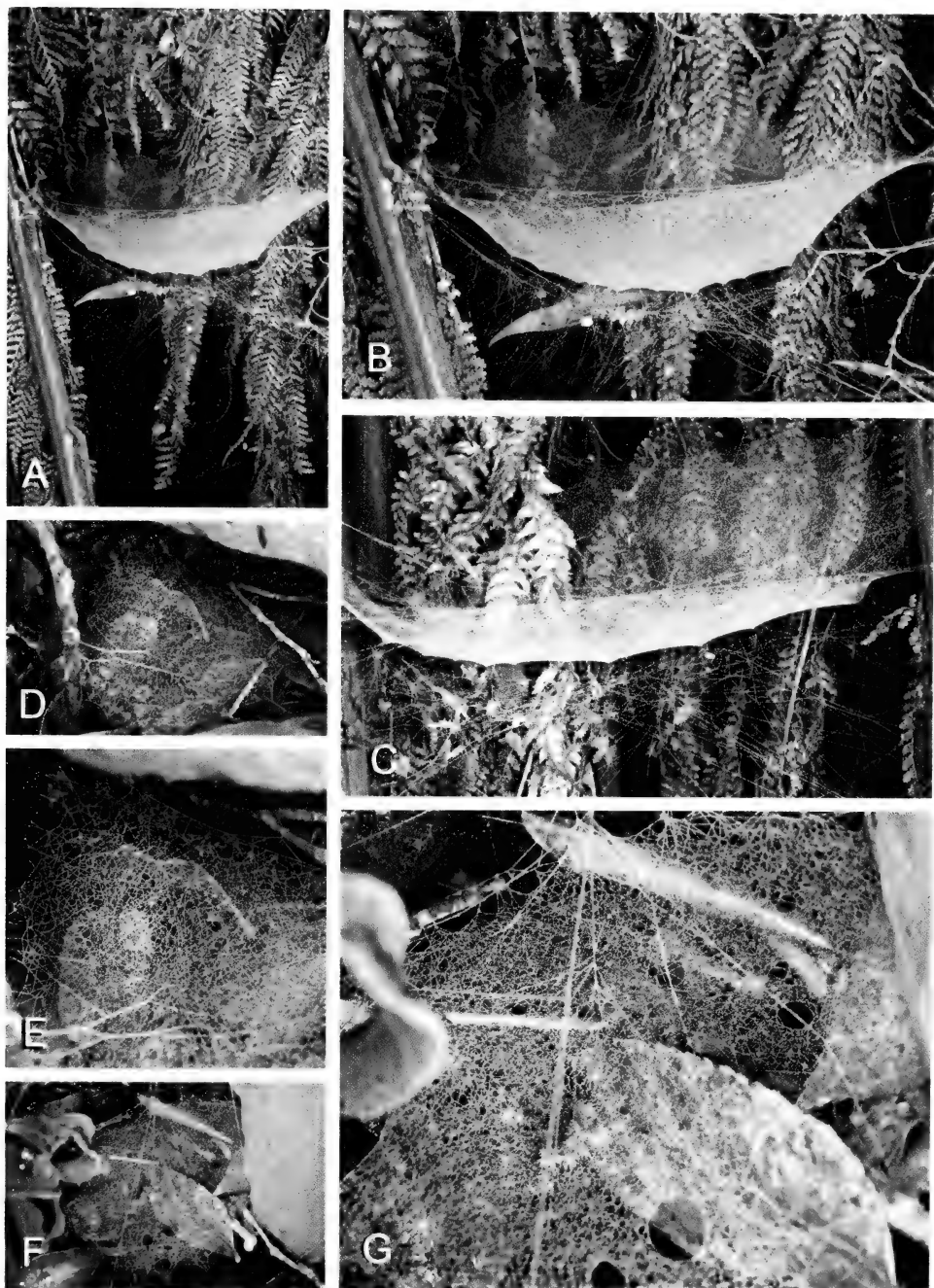


Figure 19. Australian genus 4 and *Australolinyphia* webs. (A, B) Australian genus 4 GH01. Australia, Tasmania, Weldborough Pass (DSC_0339.NEF, DSC_0343.NEF). (C) Australian genus 4 GH01. Australia, Tasmania, Weldborough Pass (DSC_0348.NEF). (D, E) *Australolinyphia remota* Wunderlich, 1976, subadult male. Australia, Queensland, Lamington National Park (GH020416_R03_11_AUS_Austral_remot.tif, GH020416_R03_12_AUS_Austral_remot.tif). (F, G) *Australolinyphia remota*, female. Australia, Queensland, Lamington National Park (GH020416_R03_15_AUS_Austral_remot.tif, GH020416_R03_16_AUS_Austral_remot.tif).

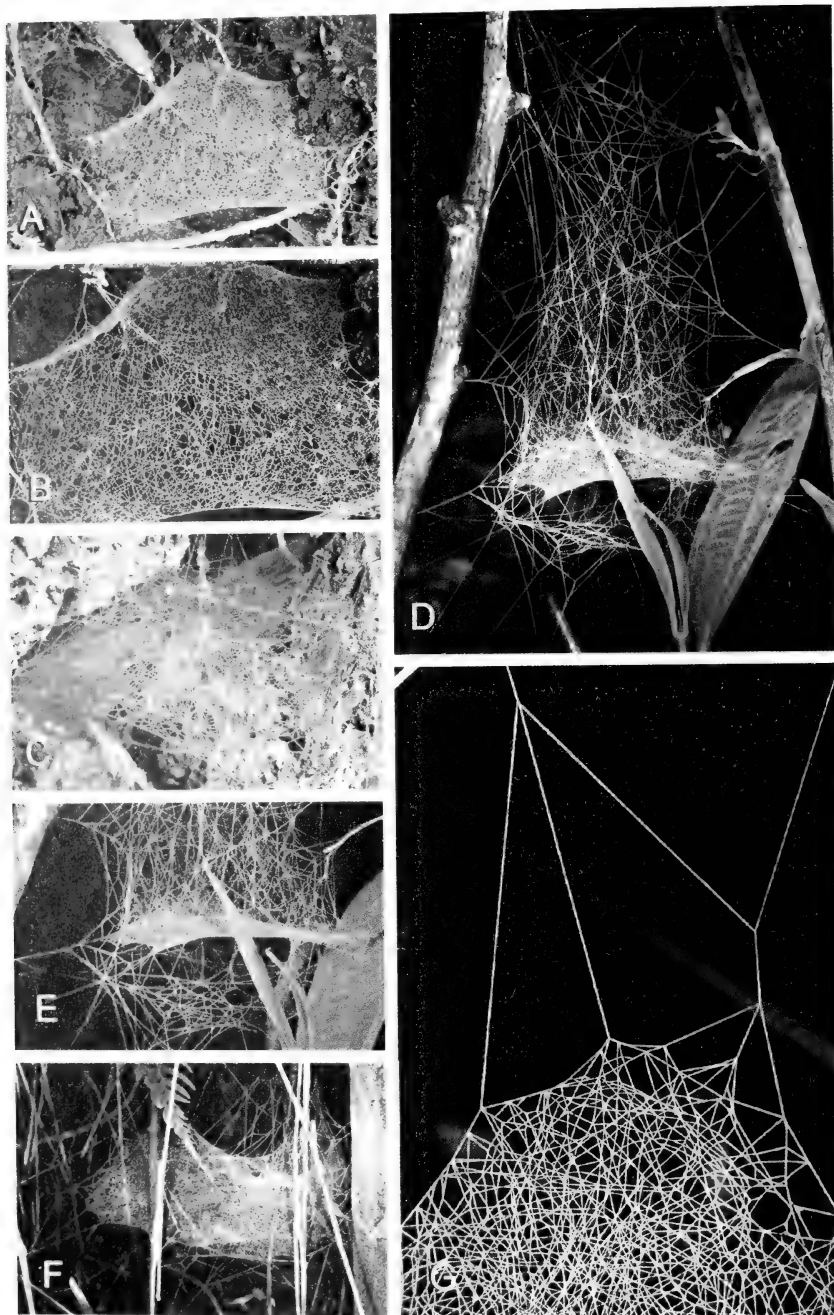


Figure 20. *Bathyphantes* and *Diplotyryon* webs. (A, B) *Bathyphantes pallidus* (Banks, 1892), subadult female. USA, Maryland, Patuxent Wildlife Research Center (GH940510_R00_21_USA_Bathy_pallid.tif, GH940510_R00_25_USA_Bathy_pallid.tif). (C) *Bathyphantes pallidus*, male. USA, Maryland, Patuxent Wildlife Research Center (GH930630_R02_07_USA_Bathy_pallid.tif). (D, E) *Diplotyryon diana* Silva-Moreira & Hormiga, 2022, female. Costa Rica, Parque Internacional La Amistad, Cerro Pittier (GH950613_R09_06_CRI_diplothy.tif, GH950615_R09_08_CRI_diplothy.tif). (F, G) *Diplotyryon diana*, female. Costa Rica, Cerro Pittier, Parque Internacional La Amistad (GH950615_R09_28_CRI_diplothy.tif, GH950615_R00_32_CRI_Diplothyron.tif).

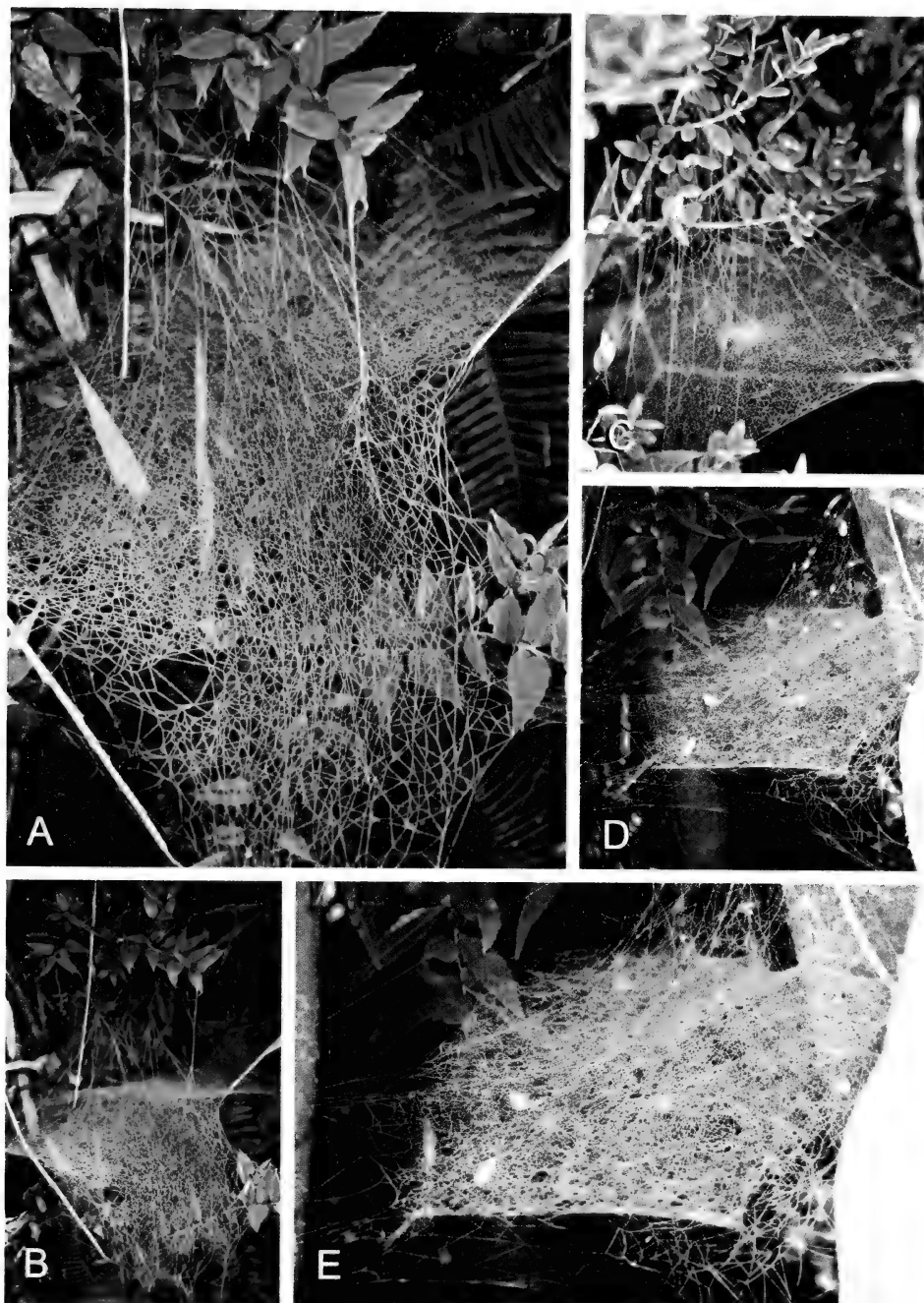


Figure 21. *Dubiaranea* webs (1). (A–E) *Dubiaranea distincta* (Nicolet, 1849) (= *Dubiaranea aysenensis* (Tullgren, 1902)), Chile, Parque Nacional Puyehue. (A, B) Female (GH001231_R04_28_CHI_Dubiar_aysens.tif, GH001231_R04_25_CHI_Dubiar_aysens.tif). (C) Male and subadult female (GH001229_R01_17_CHI_Dubiar_aysens.tif). (D, E) Female (GH010102_R06_17_CHI_Dubiar_aysens.tif, GH010102_R06_19_CHI_Dubiar_aysens.tif).

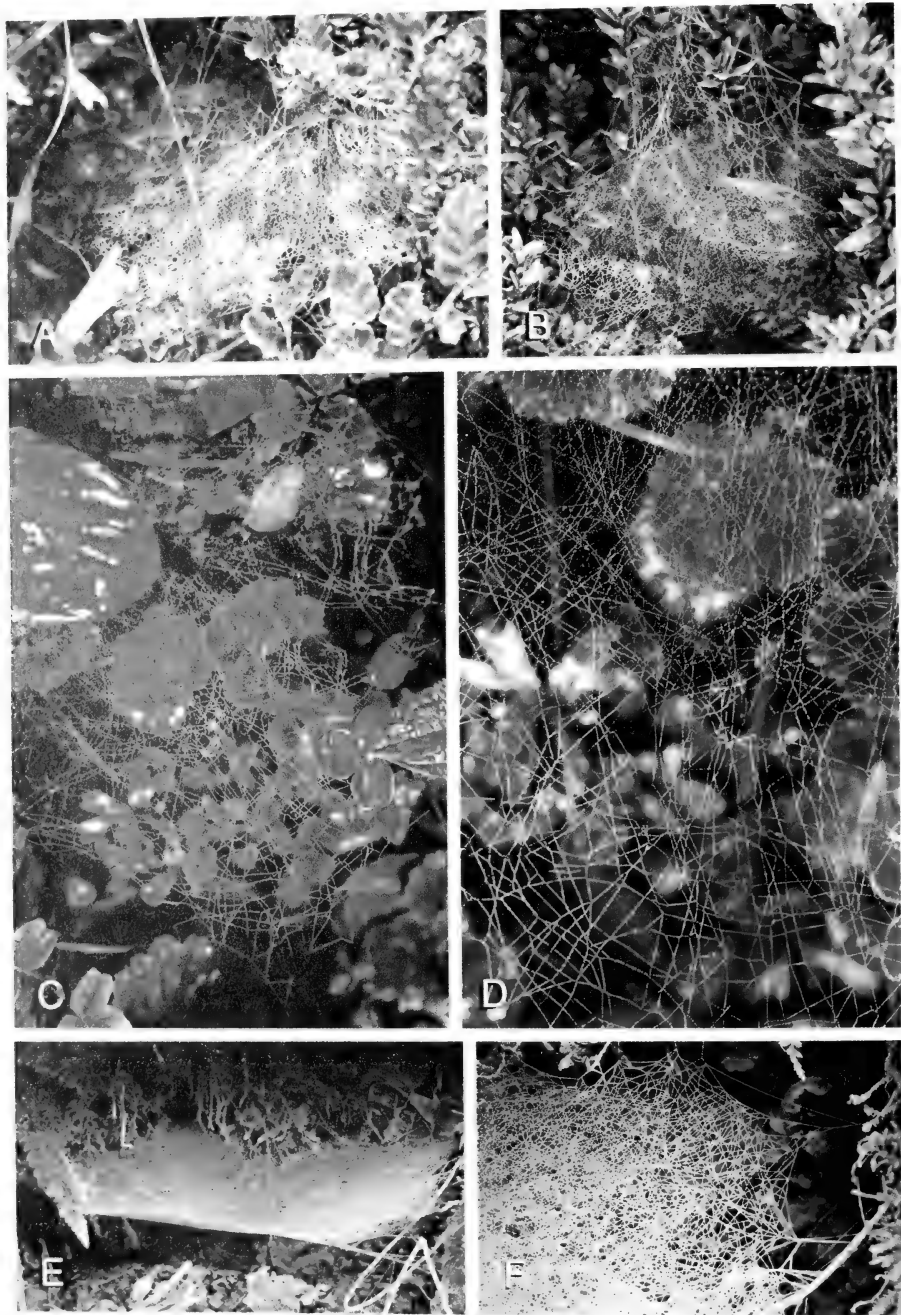


Figure 22. *Dubiaranea* webs (2). (A, B) *Dubiaranea fulgens* Millidge, 1985, female. Chile, Parque Nacional Puyehue (GH910101_R05_19_CHI_Dubiar_fulg.tif, GH010101_R05_22_CHI_Dubiar_fulg.tif). (C, D) *Dubiaranea lugubris* Millidge, 1991, female. Colombia, P.N. Purace, Laguna San Rafael (GH980215_R04_01_COL_Dubiar_lug.tif, GH980215_R04_11_COL_Dubiar_lug.tif). (E, F) *New genus MPME* sp. 1, female. Costa Rica, Cerro de la Muerte (GH930221_R02_17_CRI_Dubiar_sp.tif, GH930221_R02_10_CRI_Dubiar_sp.tif).

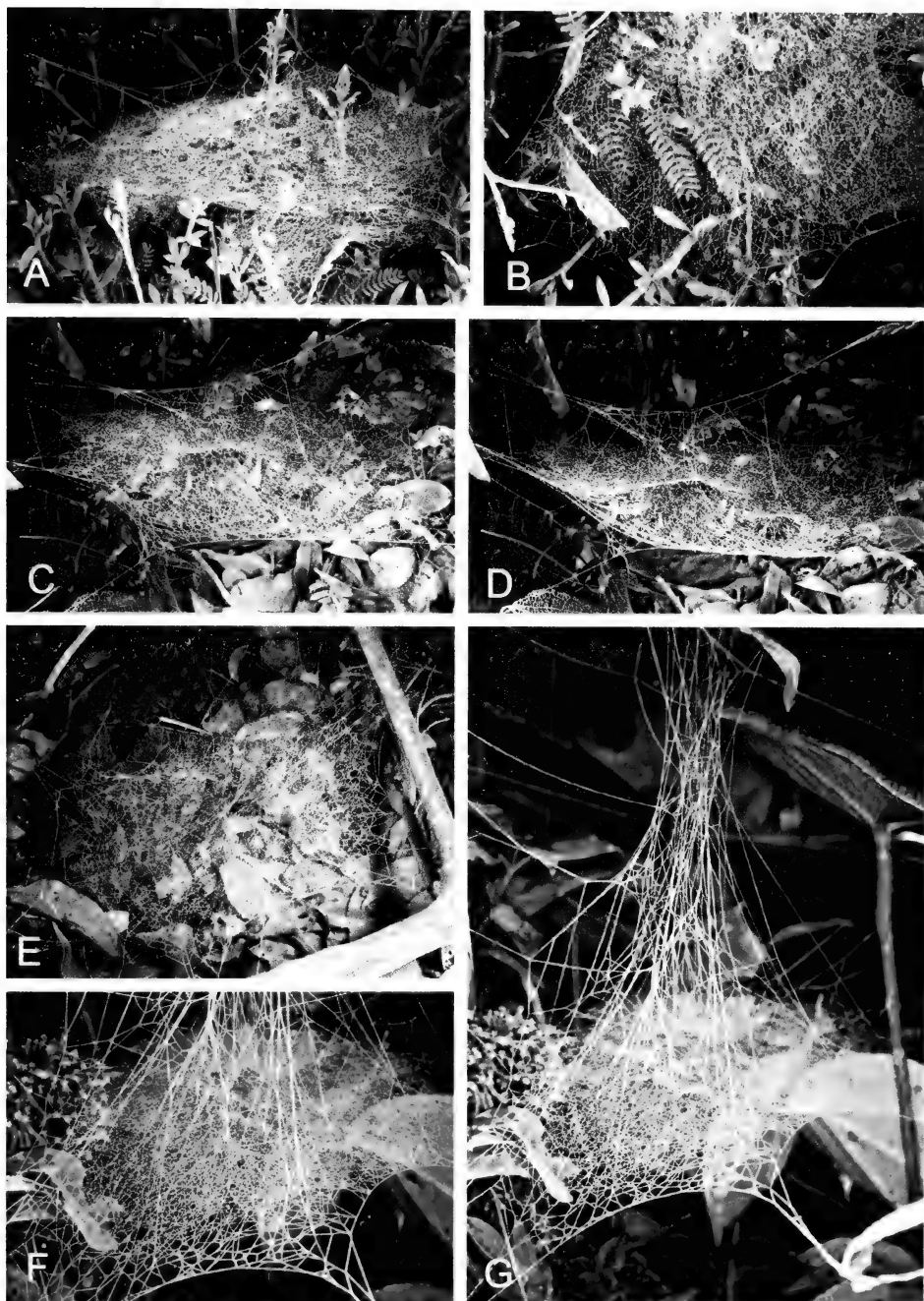


Figure 23. *Dubiaranea* webs (3). (A, B) *Dubiaranea caledonica* (Millidge, 1985), female. Chile, Monumento Nacional Contulmo (DSC_1997.NEF, DSC_2000.NEF). (C–E) *Dubiaranea insulana* Millidge, 1991, female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_416.NEF, DSC_418.NEF, DSC_428.NEF). (F, G) *Dubiaranea* sp. DE2, female. Ecuador, Napo Prov., Sierra Azul (GH960611_R01_15_ECU_Dubiar_sp_ED.tif, GH960611_R01_11_ECU_Dubiar_sp_ED.tif).



Figure 24. *Dubiaranea* webs (4). (A) *Diplothyron nubilosus* Moreira & Hormiga, 2022, female. Panama, Parque Internacional La Amistad (DSC 4011.NEF). (B) *Dubiaranea hospita* (Keyserling, 1886), female. Trinidad and Tobago, Trinidad, Brasso Seco (DSC 0554.NEF). (C) *Dubiaranea hospita* (Keyserling, 1886), female. Trinidad and Tobago, Trinidad, Brasso Seco (DSC 0544.NEF). (D, E) *Dubiaranea* sp. DE1, female. Ecuador, Napo Prov., Sierra Azul (GH960615_R04_20_ECU_Dubiar_sp.tif, GH960615_R04_23_ECU_Dubiar_sp.tif).

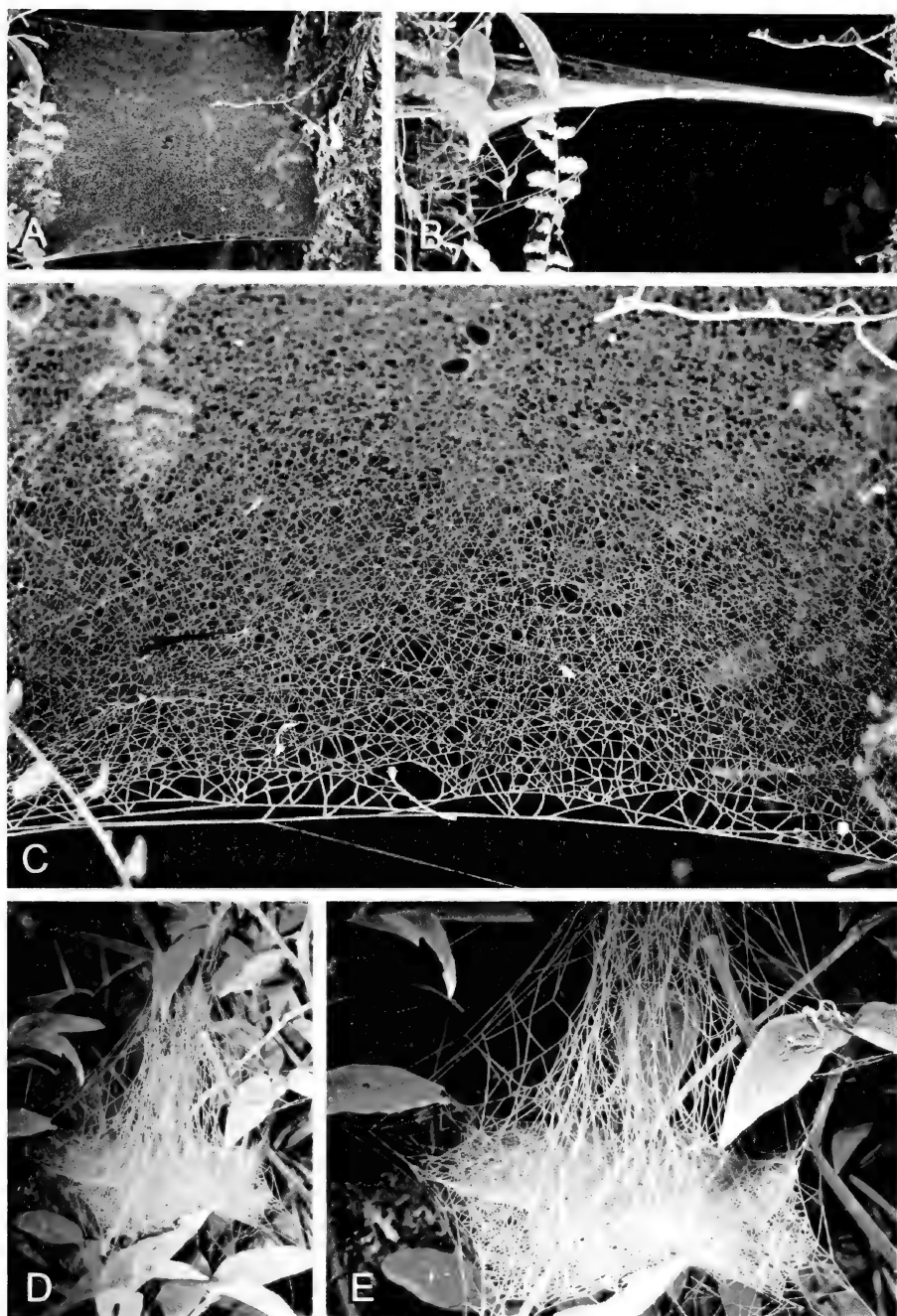


Figure 25. *Dubiaranea* webs (5). (A–C) *Dubiaranea* sp. DE1, female. Ecuador, Napo Prov., Sierra Azul (GH960610_R01_04_ECU_Dubiar_sp.tif, GH960610_R01_08_ECU_Dubiar_sp.tif, GH960610_R01_09_ECU_Dubiar_sp.tif). (D, E) *Diplothyron nubilosus* Moreira & Hormiga, 2022, female. Costa Rica, Cerro de la Muerte (GH930222_R02_23_CRI_Dubiar_spec.tif, GH930222_R02_27_CRI_Dubiar_spec.tif).

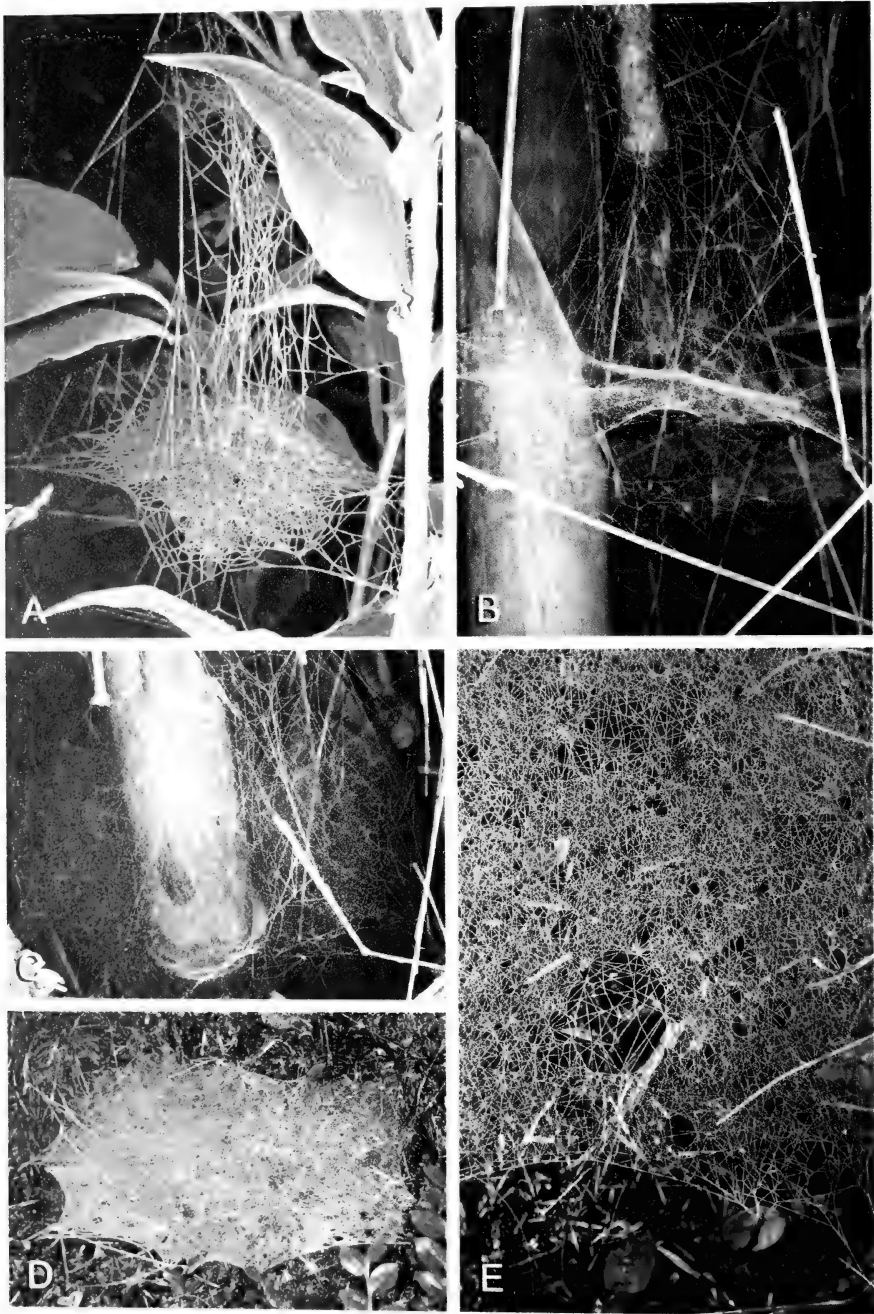


Figure 26. *Diplothyron* and *Floronia bucculenta* webs. (A) *Diplothyron nubilosus* Moreira & Hormiga, 2022, male. Costa Rica, Cerro de la Muerte (GH930222_R02_34_CRI_Dubiar_sp.tif). (B, C) *Diplothyron nubilosus* Moreira & Hormiga, 2022, male and female. Panama. Parque Internacional La Amistad (DSC_4009.NEF, DSC_4010.NEF) (note the spider on the sheet in panel C). (D, E) *Floronia bucculenta* (Clerk, 1757), female. Sweden, Tullbotorp (GH940813_R00_06_SWE_Floron_bucc.tif, GH940813_R00_09_SWE_Floron_bucc.tif).

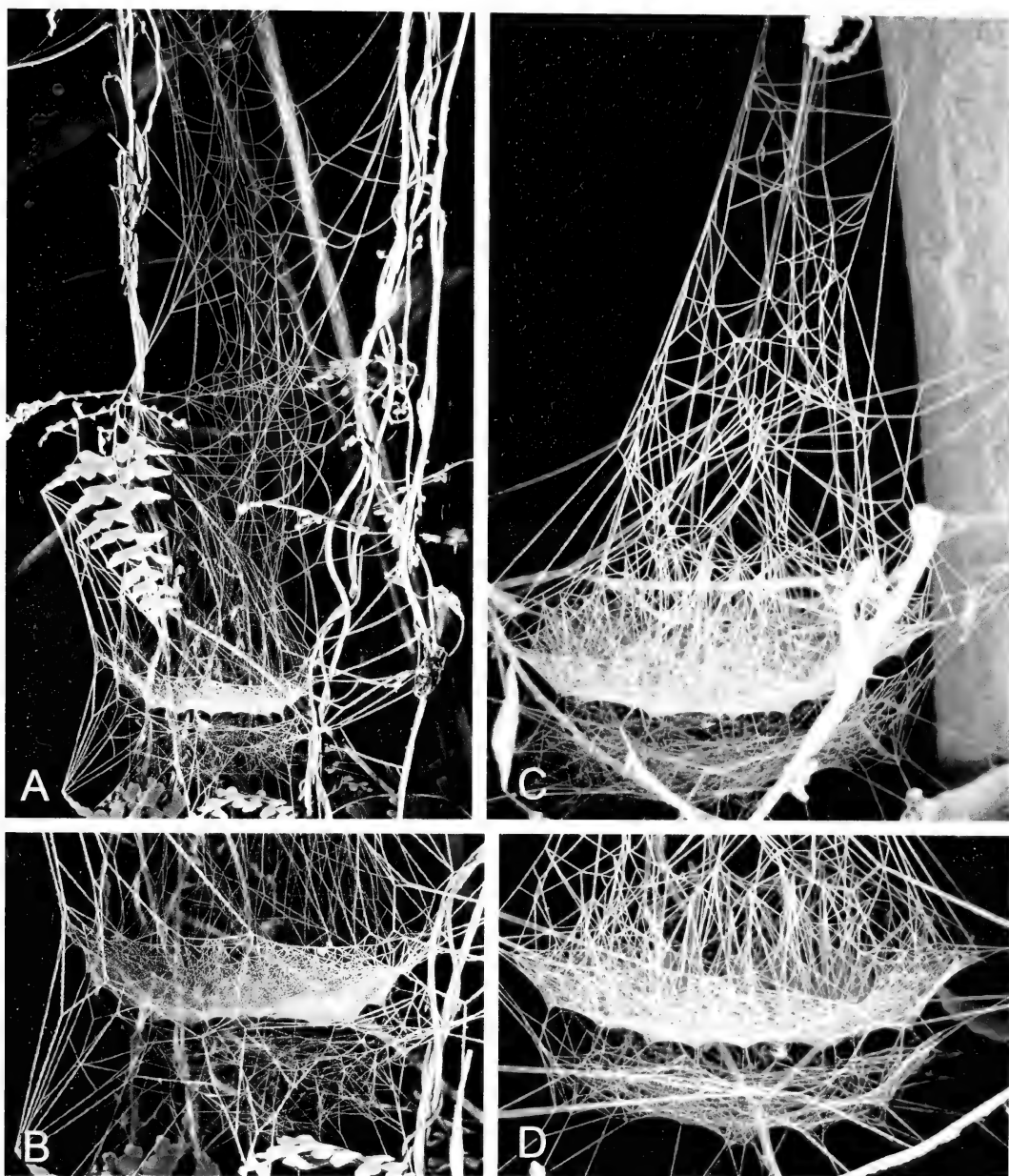


Figure 27. *Frontinella* webs. (A, B) *Frontinella* sp., female. Dominican Republic, Cachote, Sierra de Barohuco (GH050409_R02_20_DR_Frontinella.jpg, GH050409_R02_28_DR_Frontinella.jpg). (C, D) *Frontinella pyramitela* (Walckenaer, 1841), female. USA, Maryland (GH940511_R02_30_USA_Frontin_pyram.tif, GH940511_R02_32_USA_Frontin_pyram.tif).

LAETESIA (WEBS OF THREE SPECIES)

The genus *Laetesia* groups 25 described species found primarily in Australia and New Zealand, but additional Australian

species are yet to be described. The webs of all of the three species of *Laetesia* photographed were from eastern Australia and had highly elevated, dome-shaped

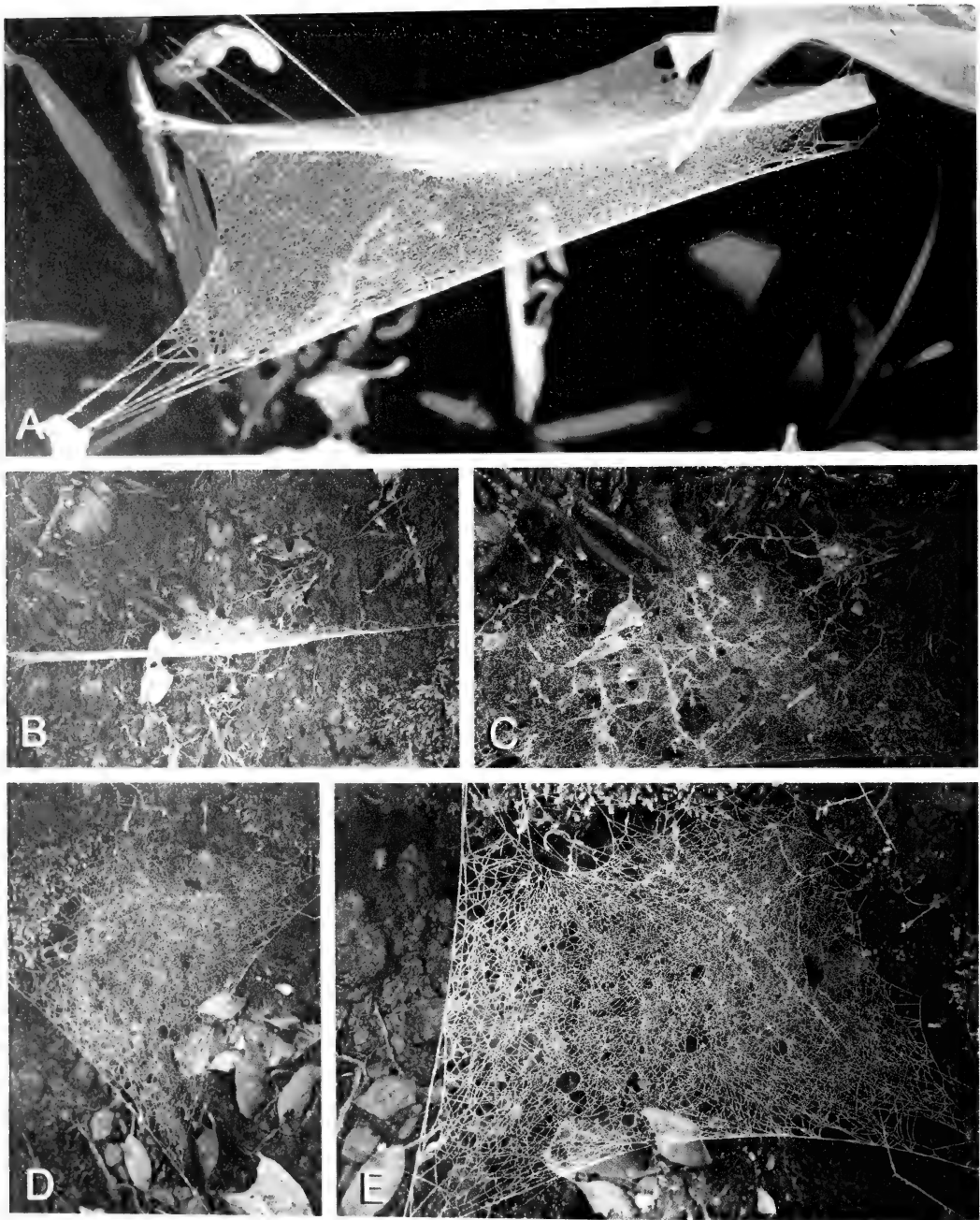


Figure 28. *Grammonota* and *Himalaphantes* webs. (A) *Grammonota* sp., juvenile. Costa Rica, La Selva (GH930403 R06_15 CRI.tif). (B, C) *Himalaphantes* sp., female. Taiwan, Nantou County, Beidong Mtn. (DSC_0991.NEF, DSC_0994). (D, E) *Himalaphantes* sp., female. Taiwan, Nantou County, Beidong Mtn. (DSC_0999.NEF, DSC_1005.NEF).

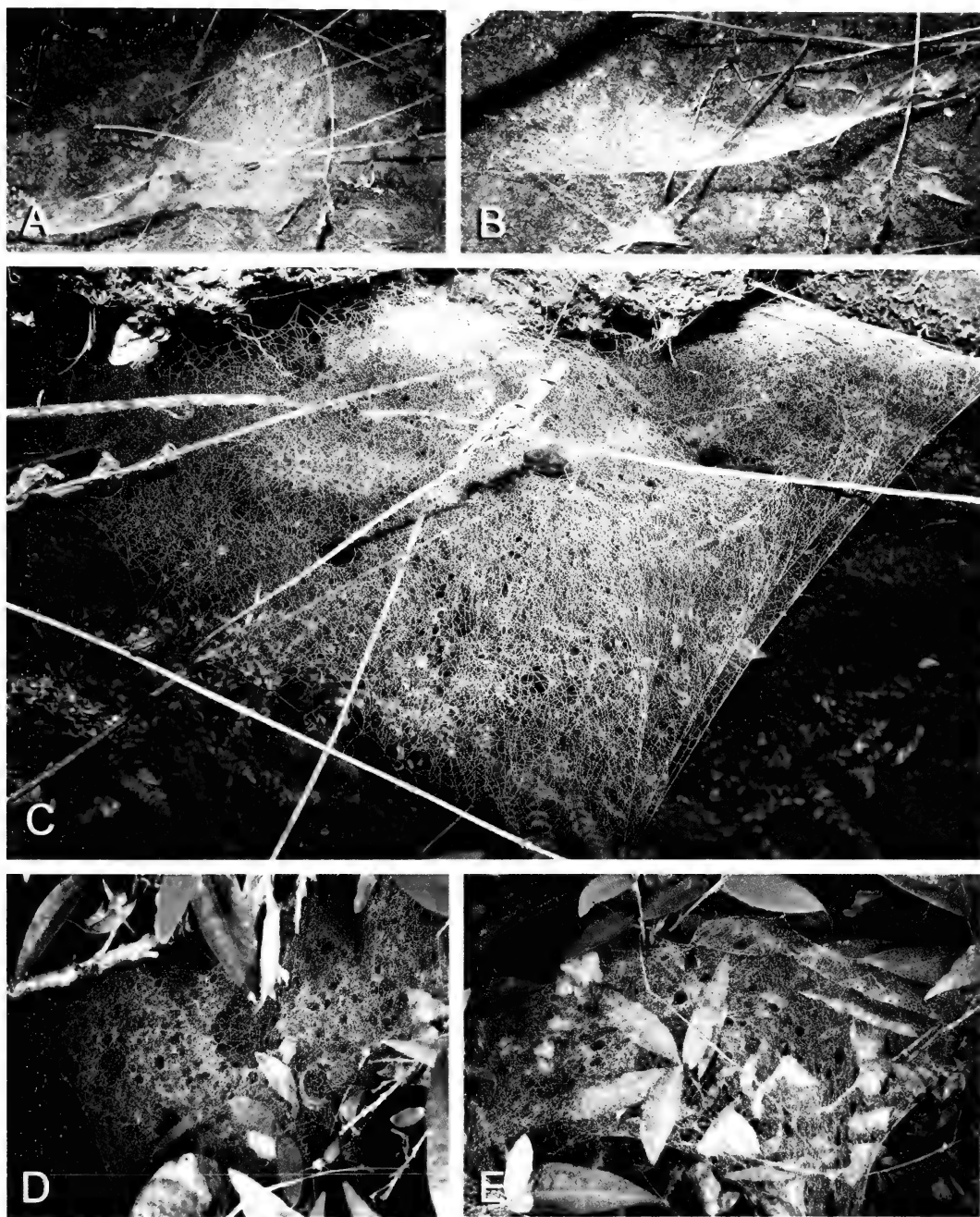


Figure 29. *Juanfermandezia* webs (1). (A–E) *Juanfermandezia melanocephala* Millidge, 1991, female. Chile, Juan Fernandez Archipelago, Alejandro Selkirk Island. (A, B) DSC_2502.NEF, DSC_2500.NEF. (C) DSC_2512.NEF. (D) DSC_2542.NEF. (E) DSC_2553.NEF.

sheets with moderate to dense upper tangles and lower tangles that were skimpy or absent. The sheets of *L. raveni* (Figs. 32, 33A, B, 34A, B) ranged from almost a conical shape with very steep sides and the peak near the underside of a plant leaf or stem (Figs. 32A–C, 33A, B) to more smoothly inclined, domed shapes (Figs. 34A–C) with no protective plant structures. The other two species also lacked protective plant structures.

LAPEROUSEA (WEBS OF THREE SPECIES)

This genus groups two described and additional undescribed species from Australia and New Zealand. The webs of the three species photographed are all from Australia; two of these species are undescribed. One web of *Laperousea blattifera* (Urquhart, 1887) (Figs. 45A, B) was a highly elevated, apparently flat, slanted dense sheet with a tall, dense upper tangle that covered the entire sheet and with almost no lower tangle. One highly elevated web of *Laperousea* sp. GH02_GH1677 (Figs. 45C, D) differed in being flat and horizontal, in having several downward-directed dimples (which were not associated with general curves in the otherwise flat sheet), a medium-sparse lower tangle far below the sheet, and a taller, equally dense upper tangle. The sheet of one web of the Tasmanian *Laperousea* sp. GH01 (Figs. 45E, F) resembled the preceding species in having a few, deeply downward-projecting dimples but was unique in being curved in a complex manner that did not fit the dome/cup/saddle/trough/flat categories (Fig. 45E). It had a sparse tangle above the sheet and a sparse tangle relatively far below the sheet (Fig. 45F).

LINYPHIA (WEBS OF TWO SPECIES)

Linyphia is a large genus (78 species are listed under this genus in the World Spider Catalog, 2022) with primarily Palearctic species; it also includes many other non-congeneric species, most of which were described in the 19th and early 20th century. We have photographed the webs

of one species and report published data from a second species. All three sheets of *Linyphia triangularis* were moderately dense and gently domed, with somewhat bumpy surfaces, the peak displaced from the center (Figs. 46A–E), and a few deep, downward-directed dimples (Figs. 46A, C). Two of the three webs were highly elevated, whereas the third was near the substrate (Figs. 46D, E). The upper tangles were not tall and only moderately dense. The lower tangles, when they could be discerned, were as wide as the sheet but were not tall. The *L. triangularis* web pictured by Nielsen (1932) had a barely domed, relatively symmetrical sheet with at least six downward-directed dimples, a tall, dense upper tangle, and a tall, moderately dense lower tangle. All four webs of *Linyphia hortensis* Sundevall, 1830, pictured by Nielsen (1932) were less elevated (they were in thick grass). Taking the statement of Benjamin and Zschokke (2004) that the webs of this species lacked tangles above and below as a guide to interpret Nielsen's otherwise somewhat unclear photograph, their sheets were weakly domed or ridged with bumpy surfaces. At least two *L. hortensis* webs had grass blades projecting through them (the typical habitat of this species is the undergrowth of woods and shady places; van Helsdingen, 1969).

MICROLINYPHIA (WEBS OF TWO SPECIES)

This genus includes 12 described species from the Holarctic region and Africa. Two webs of the Malagasy *Microlinynphia simoni* van Helsdingen, 1970, were large (note the spider in Fig. 48E), very weakly domed sheets with tall, moderately dense tangles above and moderately dense tangles below (Figs. 48A–E). One web of *Microlinynphia dana* (Chamberlin & Ivie, 1943) from North America was more clearly domed, and the upper tangle was much shorter and concentrated in the central portion of the sheet (Fig. 48F).

LEPTHYPHANTES (WEBS OF TWO SPECIES)

Leptyphantes is a large genus with more than 160 species described, mainly from the

Holarctic region and Africa. Many of the species currently placed in this genus may not be congeneric (Tanasevitch [2022] lists only seven species in *Lepthyphantes sensu stricto*). One somewhat battered web of a male of the North American *Lepthyphantes turbatrix* (O. Pickard-Cambridge, 1877) was apparently naked, sparsely meshed, slightly domed, and attached at one edge by short anchors to a tree trunk (Fig. 46F). The web of *L. minutus* (in Denmark) was built against a tree trunk, with a gently sloping sheet (possibly bent centrally like a ridge tent) that abutted on one side against the trunk and a tall dense tangle above and little or no tangle below; the spider apparently rested off the web under flakes of bark or lichens (Nielsen, 1932: fig. 409).

Low Intrageneric Diversity. *ORSONWELLES* (WEBS OF EIGHT SPECIES). The webs of eight species of *Orsonwelles* (out of a total of 13 described species), a genus endemic to the Hawaiian Islands in which spiders rest at or beyond the edge of the sheet during the day, share a distinctive trait not known in any other linyphiid—a densely meshed “runway” with many parallel lines leading from an edge of the web to the spider’s hiding place on the substrate (Fig. 62: *O. polites*; Fig. 61D: *O. malus*, lower left). Both the spiders and some of their webs are among the largest in the family Linyphiidae. Their webs were highly elevated, flat or slightly curved sheets built near large objects (except for *Orsonwelles ambersonorum* Hormiga, 2002) (Fig. 59A), with an upper tangle that varied in height and density and an absent or skimpy lower tangle that was often reduced to long dimple lines, as in *O. falstaffius* (Figs. 59D–G), *Orsonwelles ambersonorum graphicus* (Simon, 1900) (Figs. 60A–D), *O. macbeth* (Figs. 60E–G), *Orsonwelles calx* Hormiga, 2002 (Fig. 59B), and *Orsonwelles othello* Hormiga, 2002 (Figs. 61A, B). One slightly domed web of *O. malus* completely lacked a lower tangle (Fig. 61D), and another with a weak cup had a tangle below

the lower portion of the cup (Fig. 61E). The lower tangles of the flat sheets of *O. polites* varied from absent (Fig. 62D) to sparse (Fig. 62A).

SPHECOZONE (WEBS OF FOUR SPECIES)

This erigonine genus has 34 South American described species. Three webs of *Sphecozone bicolor* (Nicolet, 1849) (Figs. 63B–E), two of *Sphecozone spadicaria* (Simon, 1894) (Miller, 2007: figs. 2C, D), and another of *S. bicolor* (Miller, 2007: figs. 2E, F) were similar. All were apparently flat, medium-dense to dense sheets just above the surface of the ground that were attached to the substrate at numerous points and lacked long frame lines. They had at most only a few sparse upper tangle lines; presumably there were no lower tangle lines because the sheets were so close to the ground. The sheets of *S. bicolor* and *Sphecozone* sp. had an irregular mesh (Fig. 63F), whereas those of *S. spadicaria* were more uniform (Miller, 2007). A plant stem projected through the sheet of *S. bicolor* (Fig. 63E).

NEOMASO (WEBS OF THREE SPECIES)

The erigonine genus *Neomaso* groups 22 described species, mostly from southern South America, but several species remain to be described. The four webs of *Neomaso pollicatus* (Tullgren, 1901) (Figs. 49A–C; Miller, 2007: fig. 2A), two of *Neomaso patagonicus* (Tullgren, 1901) (Fig. 49D; Miller, 2007: fig. 1F), and one of *Neomaso* sp. (Fig. 49E) all had moderately sparsely meshed sheets that were attached at many points to the substrate. They had such irregular forms that it was difficult to characterize them or to distinguish them in the photos from sparse tangles just above the substrate. The sheets of *N. patagonicus* were especially small, with a sparse mesh and no clear tangle lines (Fig. 49D; Miller 2007: fig. 1F). At least two species of *Neomaso*, both endemic to the Juan Fernandez islands, have abandoned foraging webs (Arnedo and Hormiga, 2021). One of them is a large cursorial species (*Neomaso*

defoei (F. O. Pickard-Cambridge, 1899)), and the other (yet to be described) is presumed to be a web invader.

FRONTINELLA (WEBS OF TWO SPECIES)

Frontinella is a small genus with 10 described species found in North America, the Caribbean, and China. The webs of the two species of *Frontinella*, the North American *F. pyramitela* (Figs. 27C, D) and *Frontinella* sp. from the Dominican Republic (Figs. 27A, B), were very similar: highly elevated cup-shaped sheets with downward-projecting dimples, very tall dense upper tangles (up to more than three sheet diameters), and shorter but also dense lower tangles that were anchored by a reduced number of long lines to the substrate.

NOVAFRONTINA (WEBS OF TWO SPECIES)

This small Neotropical genus has three described species. Five webs of *N. uncata* in Costa Rica had a highly elevated, flat, dense sheet with a dense, tall upper tangle (Figs. 58A–F); the lines below the sheet formed either an open-meshed sheet (Fig. 58A) or a sparse tangle (Fig. 58F). Only a low number of lines (around 10) connected the principal sheet to the lines below; each pulled the sheet downward into a dimple (Figs. 58B, D). The relative height of the upper tangle varied dramatically; several upper tangles were tall, reaching up to about three sheet diameters above the sheet (Fig. 58A), but another (built where supports above the web may have been lacking) was only just over half of the sheet diameter (Figs. 58G, H). The upper tangle of this web appeared to have two portions: most lines in the upper portion were more nearly horizontal, whereas most lines in the lower portion were nearly vertical, attached below to the principal sheet and above to the horizontal lines. One of the *N. uncata* webs documented in the same area as those just described had a smaller irregular sheet under the main sheet (possibly a remnant of a previous sheet) and a loose mesh of a few irregular lines between the two sheets.

Three webs of *Novafrontina* sp. (from Brazil) were similar, in being flat with tall, dense upper tangles. Lines in their lower tangles did not form sheets, however, and two of the lower tangles had sagging fragments of sheets that appeared to be remnants of previous sheets. One sheet was weakly cup-shaped (Figs. 57A, B), whereas another was flat (Figs. 57D, E); one lacked frame lines along two sides where a large number of lines attached the sheet directly to the substrate (Fig. 57C). (In contrast, it appeared that none of the *N. uncata* webs lacked frames, but this detail was difficult to see.)

JUANFERNANDEZIA (WEBS OF TWO SPECIES)

The genus *Juanfernandezia* is endemic to the Juan Fernandez islands and includes two species, one of them undescribed (Arnedo and Hormiga, 2021). Three webs of *J. melanocephala* (Selkirk Island) (Figs. 29A–E) and five of *Juanfernandezia* sp. (Robinson Crusoe Island) (Figs. 30A–E) were very similar. All were densely meshed flat sheets close to but slightly above the forest floor, lacking tangles or long frame lines with only a few attachments to the substrate. Several sheets of both species had apparent repairs of holes (e.g., Figs. 29C–E; an especially large repair in Fig. 30B). One *J. melanocephala* sheet had a stem protruding through it (Fig. 29C).

AUSTRALIAN GENUS 3 (WEBS OF TWO SPECIES)

We have photographed the webs of two of the species in this undescribed Australian genus that groups an unknown number of species. Both species had elevated, very dense, asymmetrically curved sheets with dense lower tangles. All but perhaps one web of GH01 (Fig. 18C) were apparently sheltered next to tree trunks. The lower tangle of sp. GH02 was much more dense under the central, lowest portion of the sheet (Fig. 18E) (presumably where the spider rested). The sheet of one GH01 web curved both upward and downward on different sides (Fig. 18B), whereas the two GH02 webs were both cup-shaped, al-

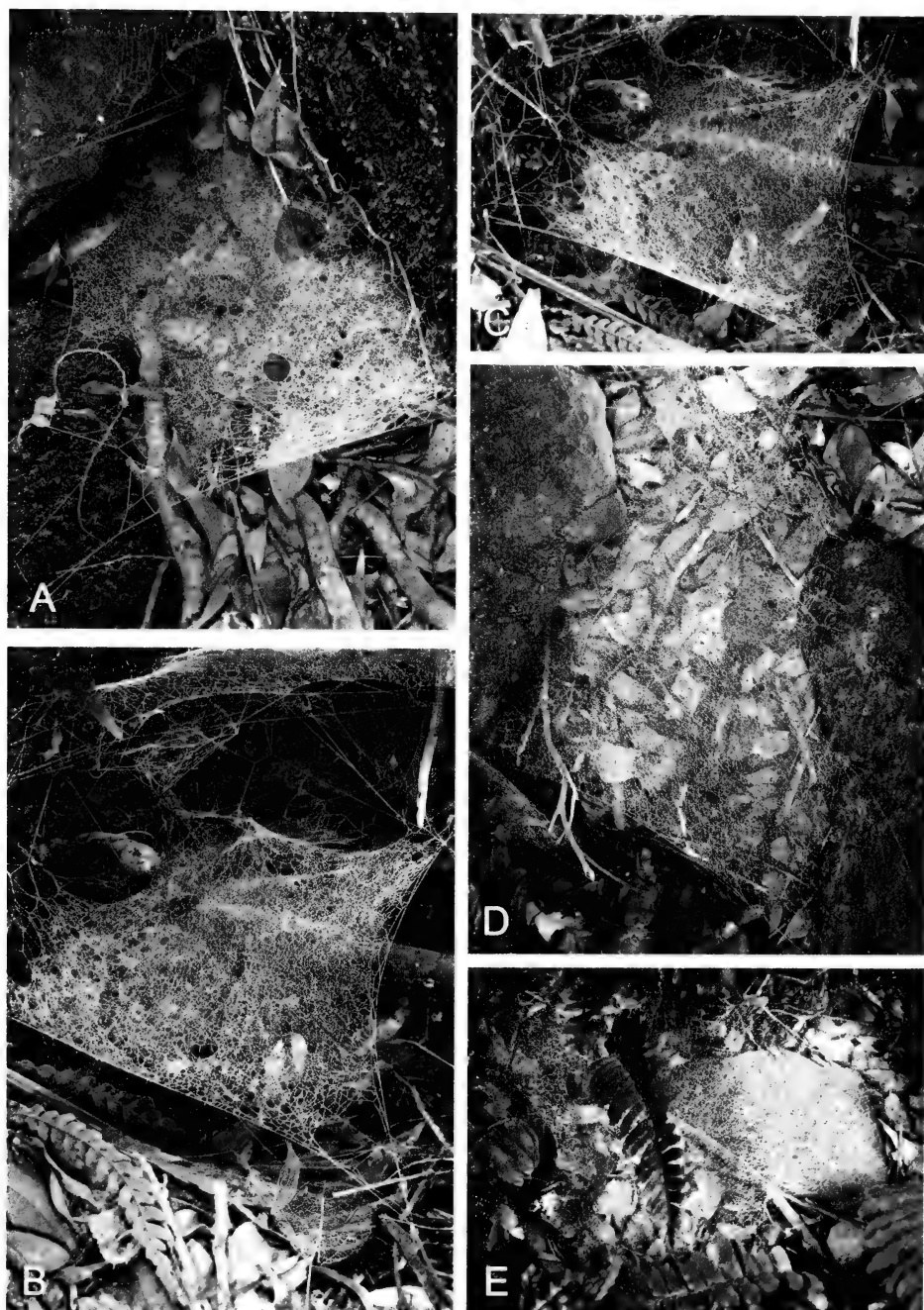


Figure 30. *Juanfermandezia* webs (2). (A–E) *Juanfermandezia* n. sp., female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island. (A) DSC_0004.NEF. (B) DSC_0423.NEF. (C) DSC_0430.NEF. (D) DSC_0011.NEF. (E) DSC_0331.NEF.

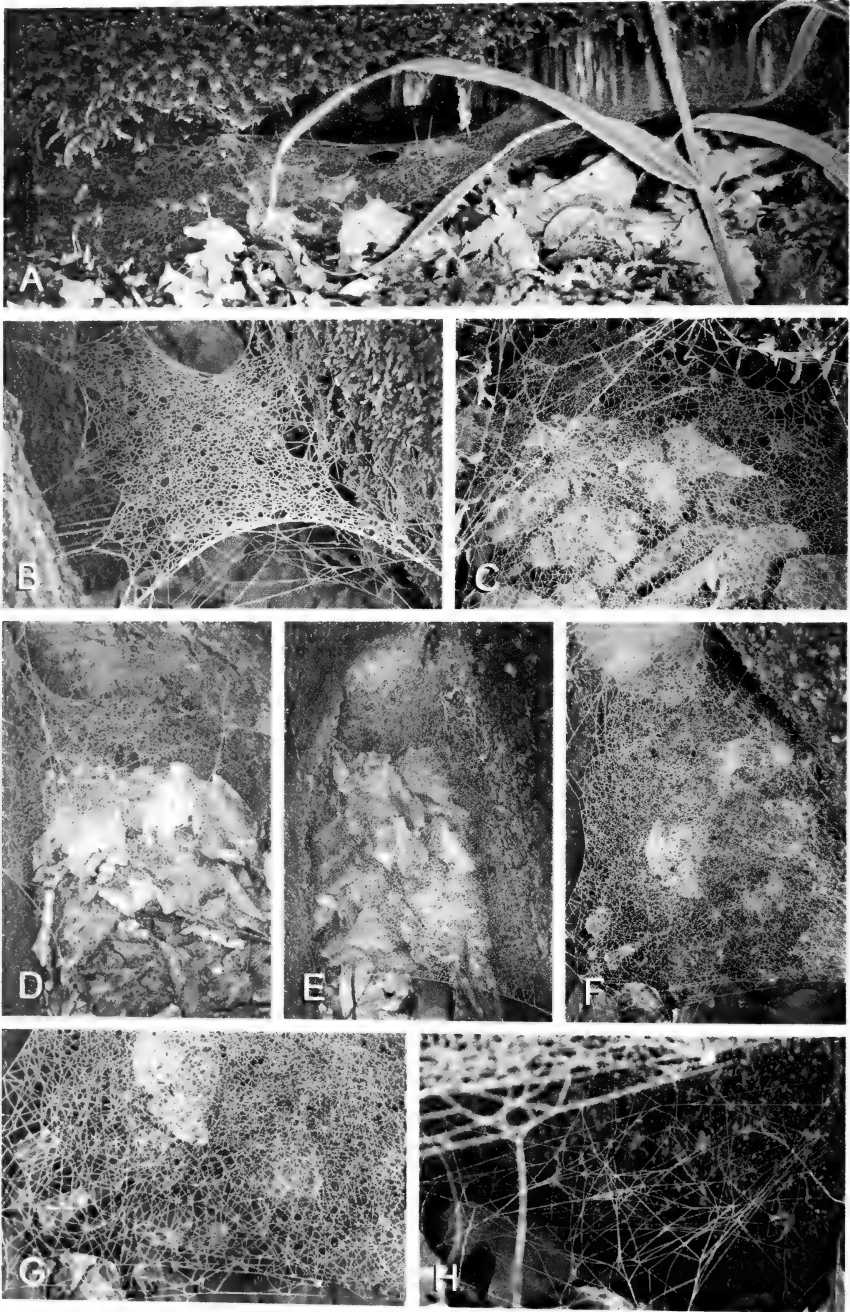


Figure 31 *Labulla* webs. (A-H) *Labulla thoracica* (Wider, 1834), Hestehaven Forest, Denmark. (A) Female, GH940830_R04_07_DEN_Labull_thorac.tif. (B) Male, female, GH940829_R04_33_DEN_Labull_thorac.tif. (C) Male, female, GH940830_R04_05_DEN_Labull_thorac.tif. (D) Male, female, GH940831_R04_34_DEN_Labull_thorac.tif. (E) Female, GH940901_R04_24_DEN_Labull_thorac.tif. (F-H) Male, female, GH940901_R04_06_DEN_Labull_thorac.tif; female, GH940901_R04_07_DEN_Labull_thorac.tif; male, female, GH940901_R04_08_DEN_Labull_thorac.tif.

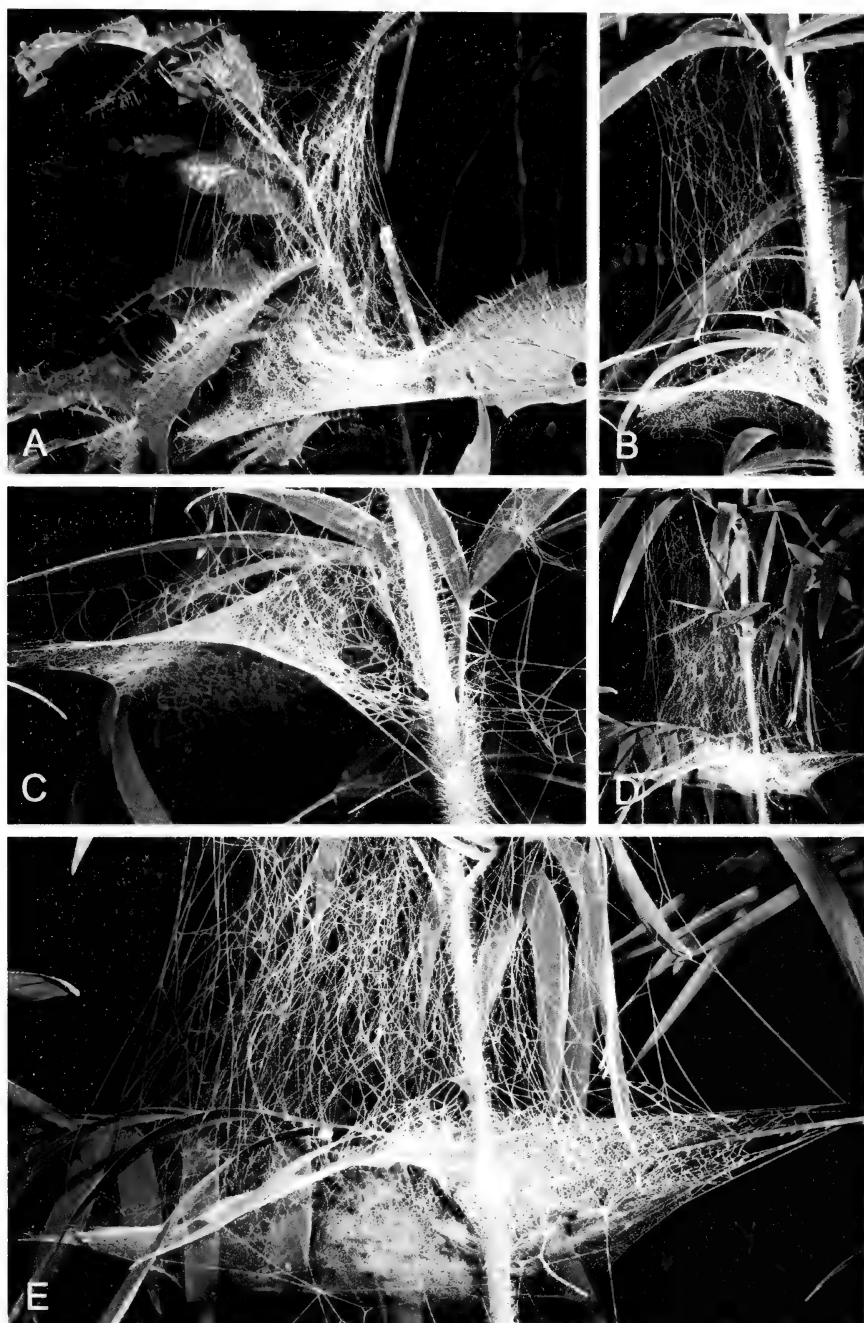


Figure 32. *Laetesia* webs (1). (A–H) *Laetesia raveni* Hormiga & Scharff, 2014, female. Australia, New South Wales, Dorrigo National Park. (A) DSC_2834.NEF. (B, C) DSC_2808.NEF, DSC_2804.NEF. (D, E) DSC_2824.NEF, DSC_2828.NEF.

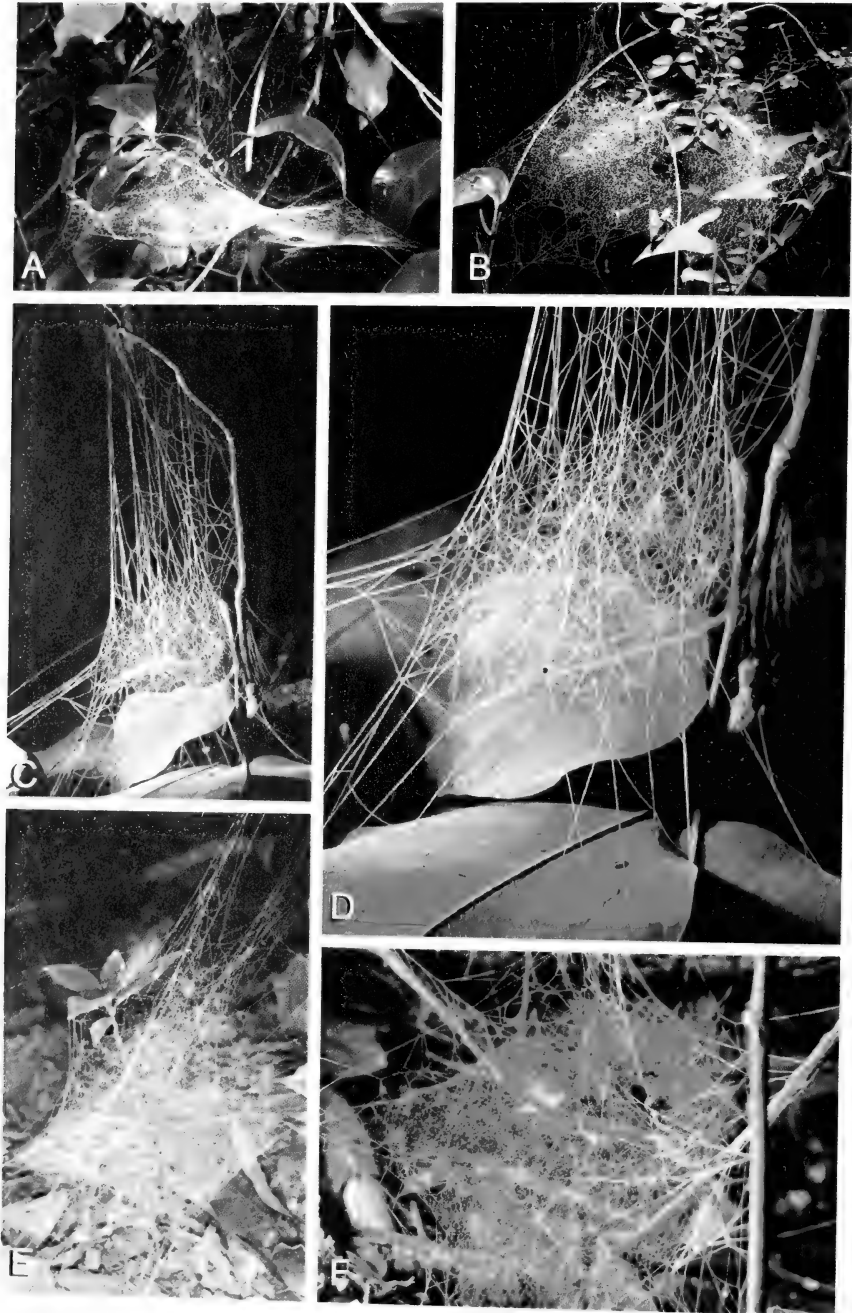


Figure 33. *Laetesia* webs (2). (A, B) *Laetesia raveni* Hormiga & Scharff, 2014, female. Australia, Victoria (DSC_1312.NEF, DSC_1312.NEF). (C, D) *Laetesia* GH01, female. Australia, Queensland, Cape Tribulation National Park (GH920726_R05_02_AUS_Laetesia.tif, GH920726_R05_04_AUS_Laetesia_sp.tif). (E) *Laetesia* GH01, female. Australia, Queensland, Cape Tribulation National Park (GH020425_R12_02_AUS.TIF). (F) *Laetesia* GH01, female. Australia, Queensland, Cape Tribulation National Park (GH920726_R05_34_AUS_Laetesia_sp.tif).

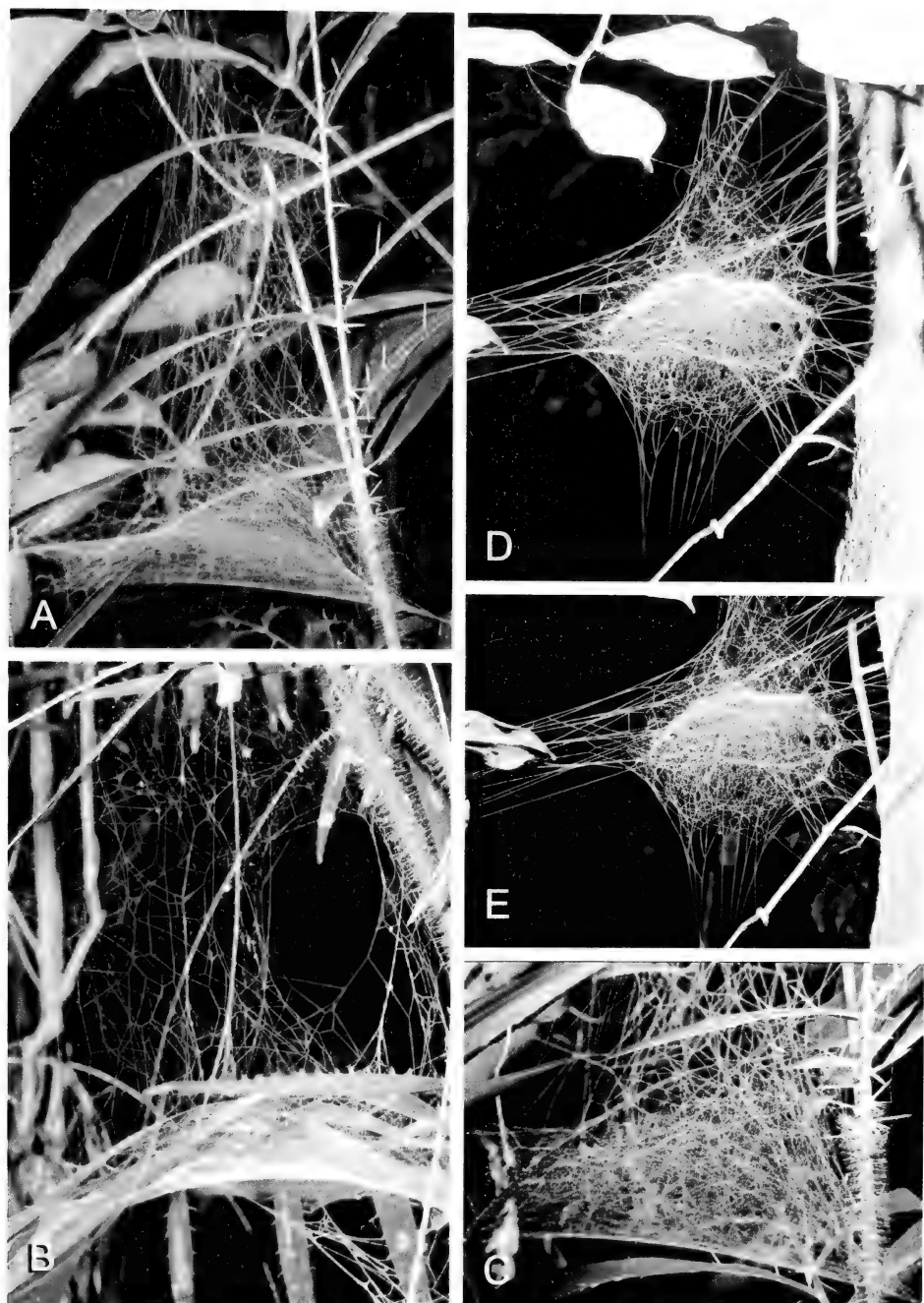


Figure 34. *Laetesia* webs (3). (A, C) *Laetesia raveni* Hormiga & Scharff, 2014, male, Australia, Queensland, Bina Burra (GH020418_R06_05_AUS.tif, GH020418_R06_07_AUS.tif). (B) *Laetesia raveni* Hormiga & Scharff, 2014, female, Australia, Queensland, Bina Burra (GH020418_R05_33_AUS.tif). (D, E) *Laetesia* GH02, male, Australia, Queensland, Atherton Tablelands (GH020420_R07_03_AUS.tif, GH020420_R06_35_AUS.tif).

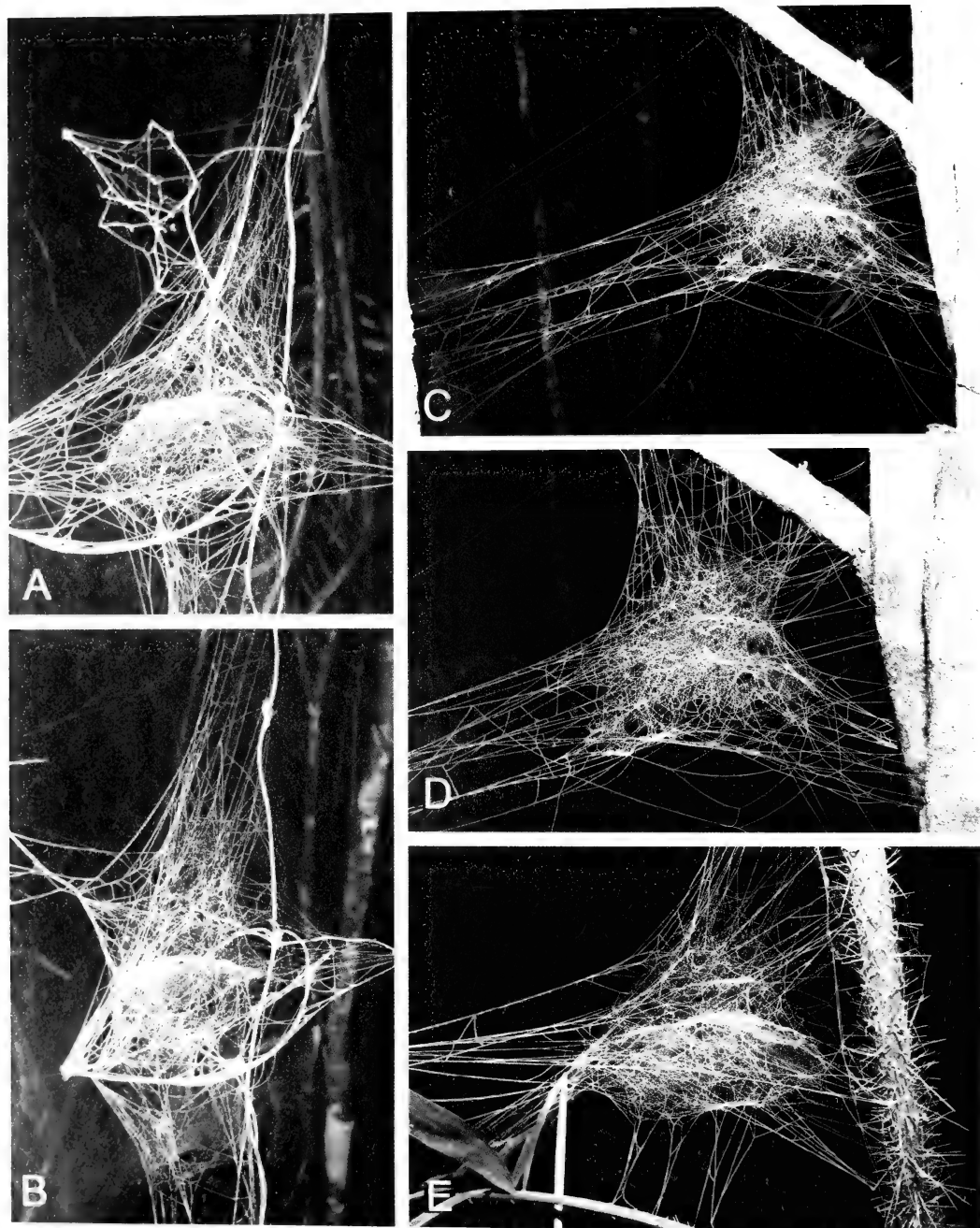


Figure 35. *Laetesia* webs (4). (A, B) *Laetesia* GH02, female. Australia, Queensland, Atherton Tablelands (DSC_8056.NEF, DSC_8051.NEF). (C, D) *Laetesia* GH02, male, female. Australia, Queensland, Atherton Tablelands (DSC_8040.NEF, DSC_8045.NEF). (E) *Laetesia* GH02, female. Australia, Queensland, Atherton Tablelands (DSC_8049.NEF).

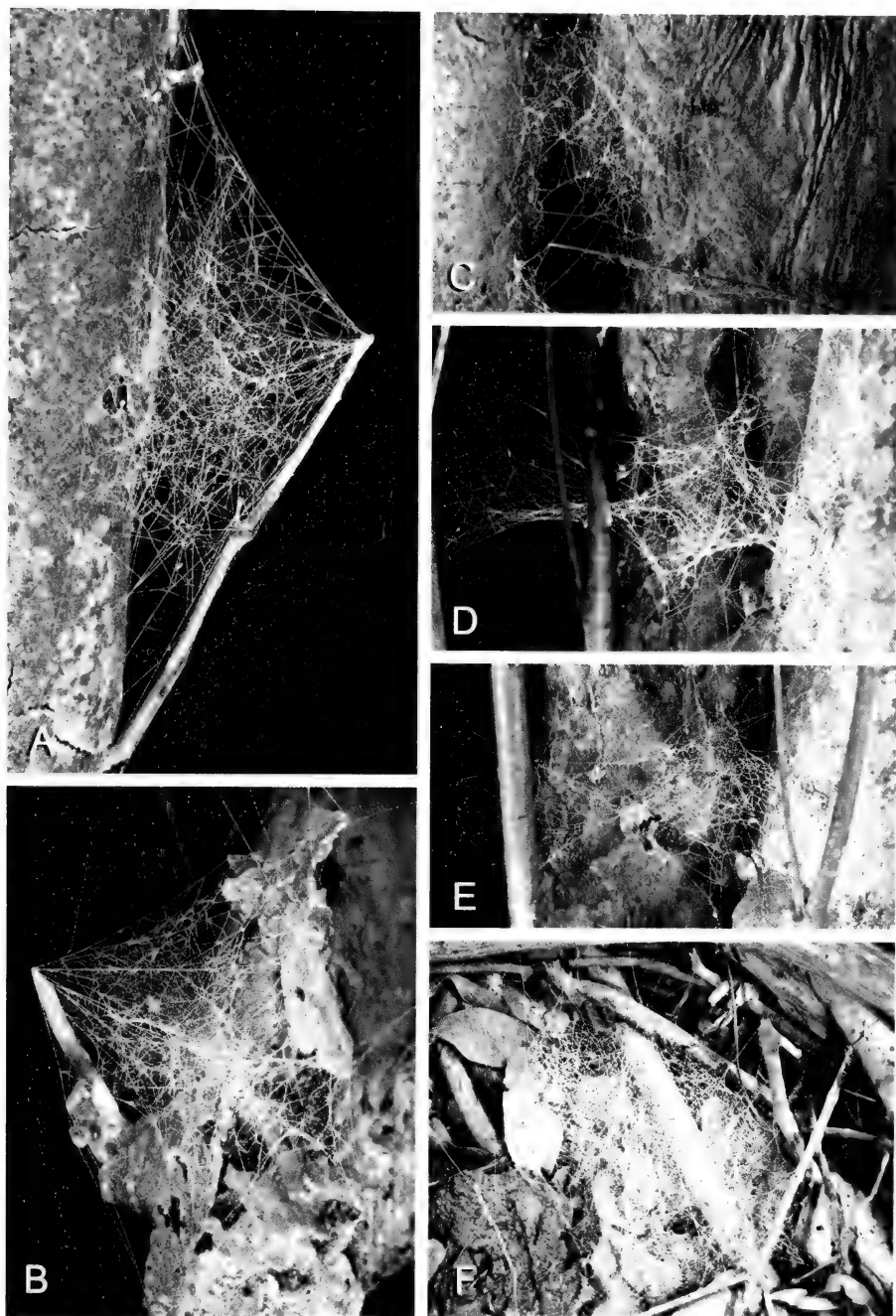


Figure 36. *Laminacauda* webs (1). (A) *Laminacauda ansoni* Millidge, 1991, female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0035.NEF). (B) *Laminacauda ansoni* Millidge, 1991, male. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0020.NEF). (C) *Laminacauda ansoni*, male. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0052.NEF). (D, E) *Laminacauda ansoni*, female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0443.NEF, DSC_0438.NEF). (F) *Laminacauda* sp. ("chps"). Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0304.NEF).

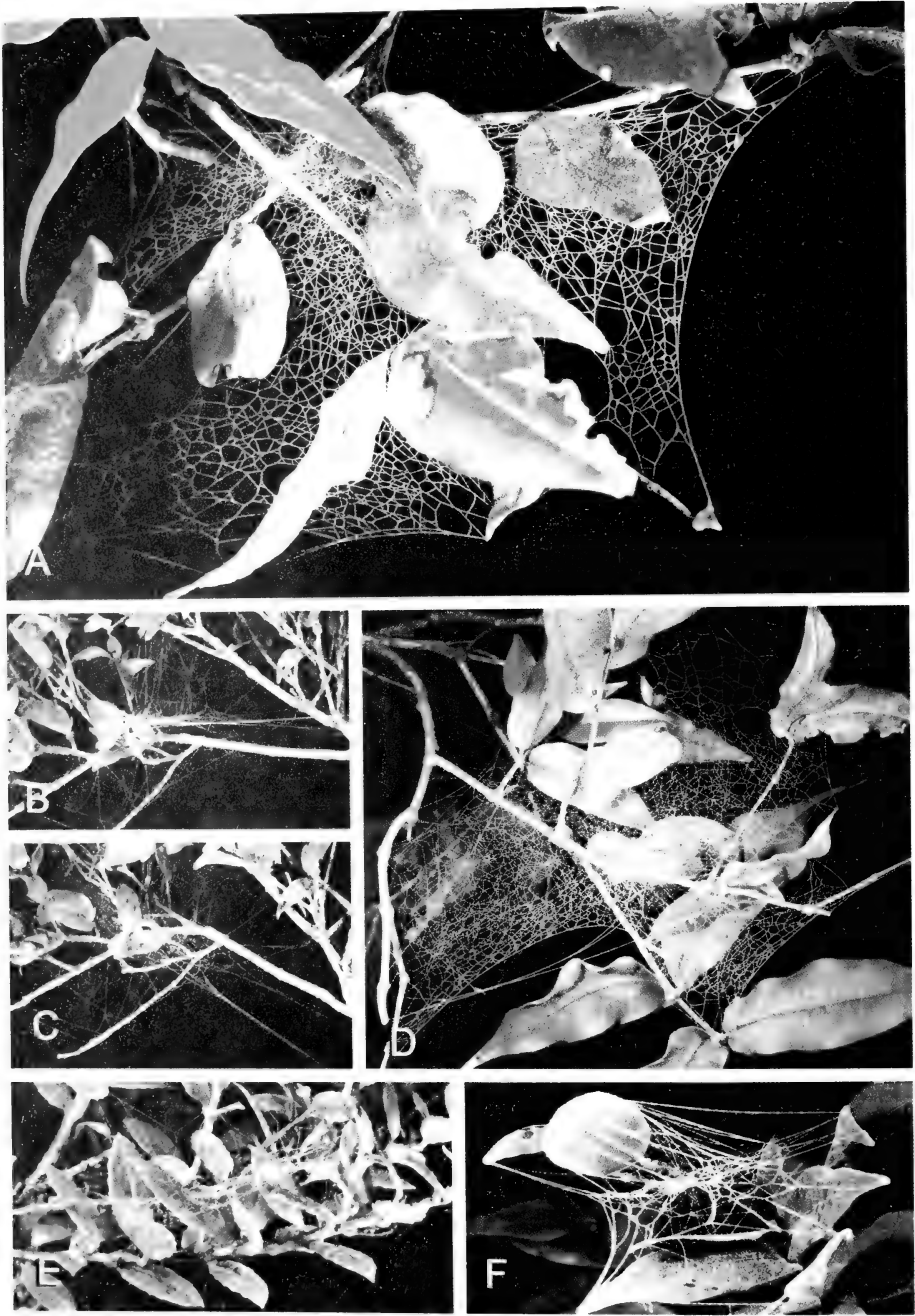


Figure 37. *Laminacauda* webs (2). (A) *Laminacauda malkini* Millidge, 1991, female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0709.NEF). (B, C) *Laminacauda malkini*, female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0584.NEF, DSC_0587). (D) *Laminacauda malkini*, female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0712.NEF). (E, F) *Laminacauda malkini*, subadult female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0575.NEF, DSC_0578)

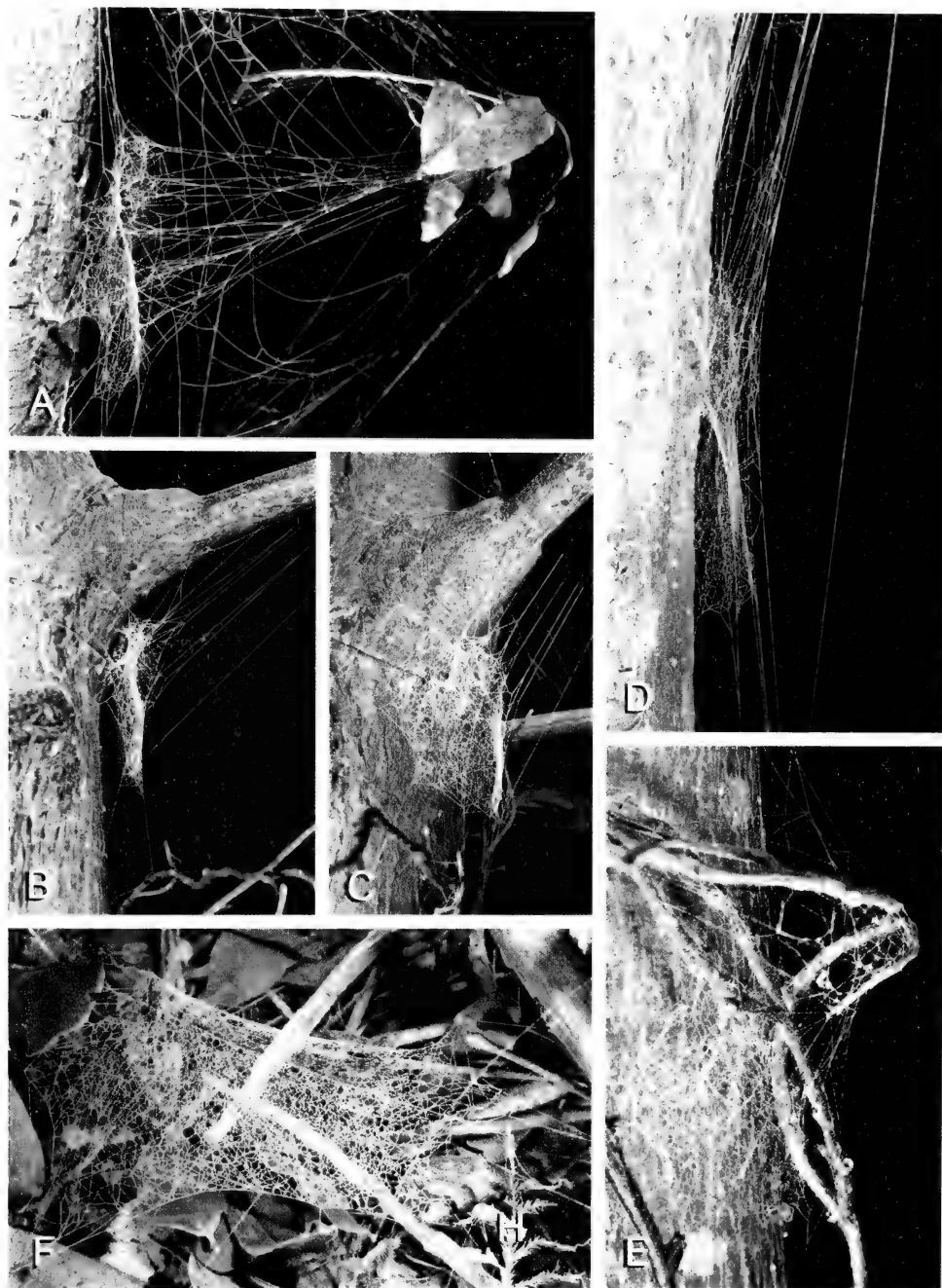


Figure 38. *Laminacauda* webs (3). (A) *Laminacauda rubens* Millidge, 1991, male, Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0046.NEF). (B, C) *Laminacauda rubens*, female, Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0020.NEF, DSC_0026.NEF). (D) *Laminacauda rubens*, female, Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0001.NEF). (E) *Laminacauda rubens*, male, Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0318.NEF). (F) *Laminacauda* sp. ("chdes"), male, Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0299.NEF).

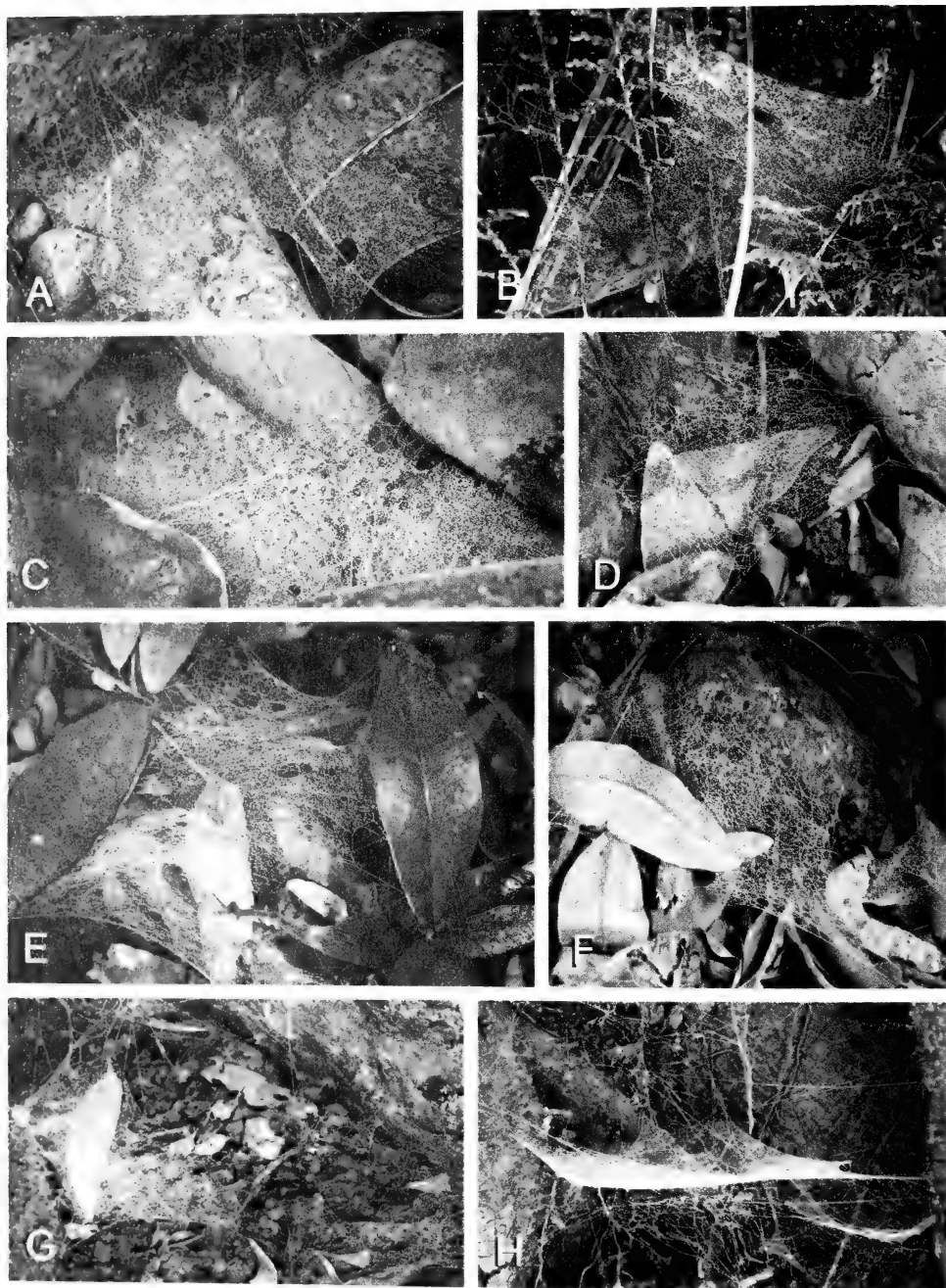


Figure 39. *Laminacauda* webs (4). (A) *Laminacauda propinqua* Millidge, 1991, female, Chile, Juan Fernandez Archipelago, Alejandro Selkirk Island (DSC 2495 NEF). (B) *Laminacauda propinqua*, female, Chile, Juan Fernandez Archipelago, Alejandro Selkirk Island (DSC 2519 NEF). (C) *Laminacauda propinqua* (no sex info), Chile, Juan Fernandez Archipelago, Alejandro Selkirk Island (DSC 2496 NEF). (D) *Laminacauda propinqua*, female, Chile, Juan Fernandez Archipelago, Alejandro Selkirk Island (DSC 2532 NEF). (E) *Laminacauda propinqua*, female, Chile, Juan Fernandez Archipelago, Alejandro Selkirk Island (DSC 2537 NEF). (F) *Laminacauda propinqua*, female, Chile, Juan Fernandez Archipelago, Alejandro Selkirk Island (DSC 2529 NEF). (G) *Laminacauda propinqua*, male, Chile, Juan Fernandez Archipelago, Alejandro Selkirk Island (DSC 2535 NEF). (H) *Laminacauda tuberosa* Millidge, 1991, Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC 0299 NEF).

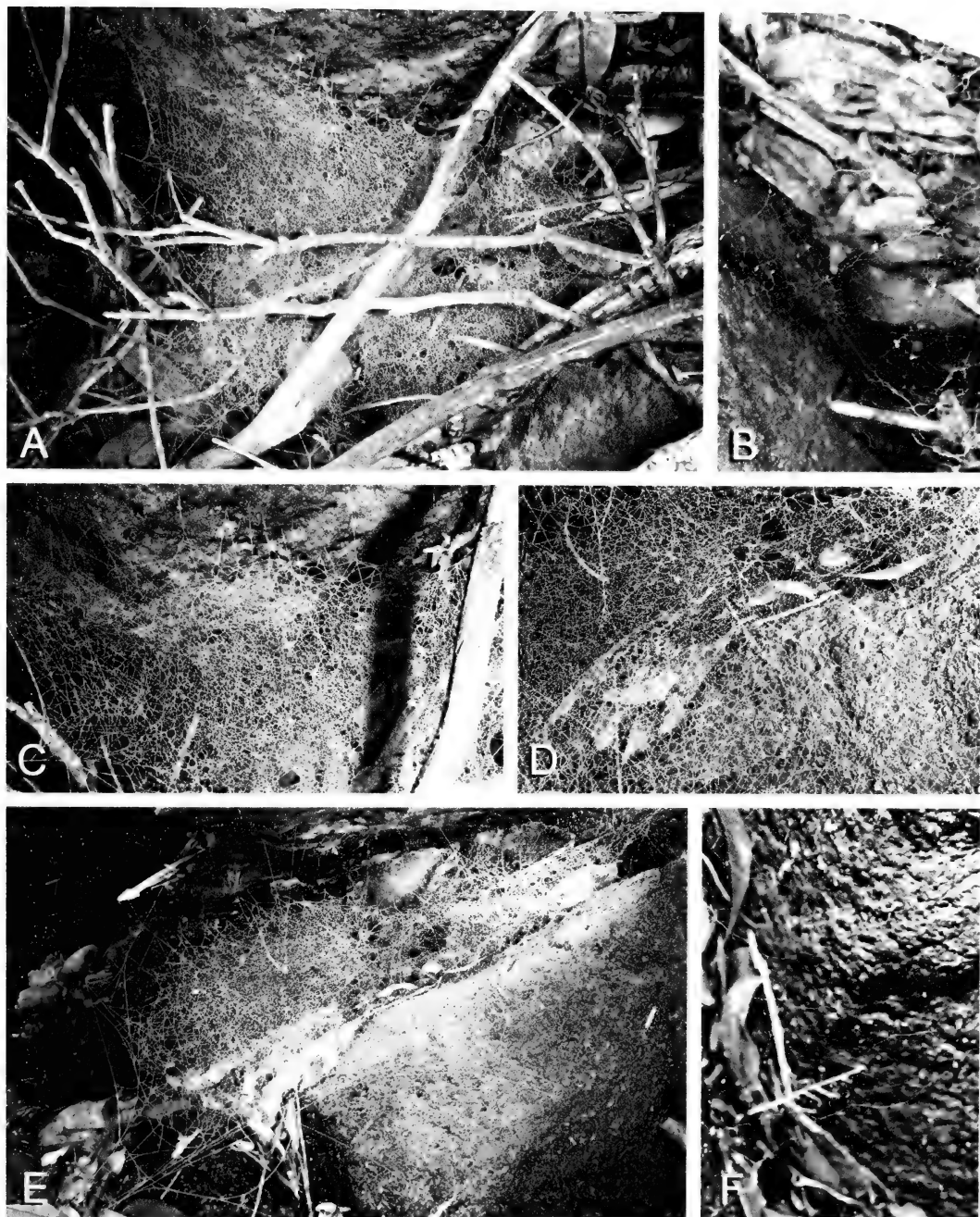


Figure 40. *Laminacauda* webs (5). (A–C) *Laminacauda magna* Millidge, 1991, female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island. (B) Undusted, detail showing glistening silk (DSC_0674.NEF, DSC_0672.NEF, DSC_0678.NEF). (D, E) *Laminacauda magna*, female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island. (F) Undusted, detail showing glistening silk (DSC_0682.NEF, DSC_085.NEF, DSC_0680.NEF).



Figure 41. *Laminacauda* webs (6). (A, B) *Laminacauda magna* Millidge, 1991, female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0018.NEF, DSC_0013.NEF). (C, D) *Laminacauda magna* (no sex info). Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0103.NEF, DSC_0105.NEF). (E) *Laminacauda magna*, female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0093.NEF).

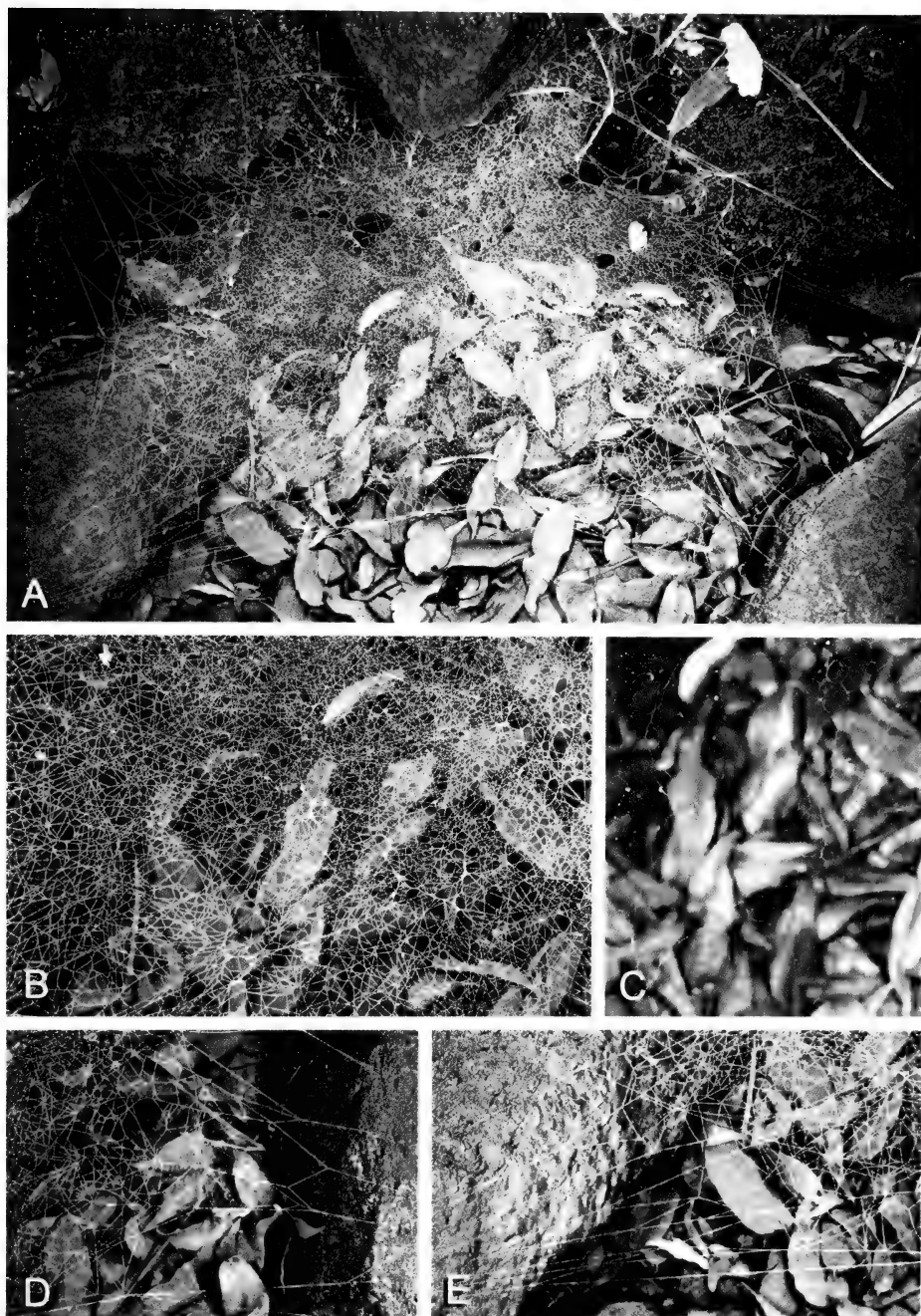


Figure 42. *Laminacauda* webs (7). (A–E) *Laminacauda magna* Millidge, 1991, female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island. (B) Undusted, detail showing glistening silk (DSC_0692.NEF, DSC_0694.NEF, DSC_0690.NEF, DSC_0697.NEF, DSC_0696.NEF).

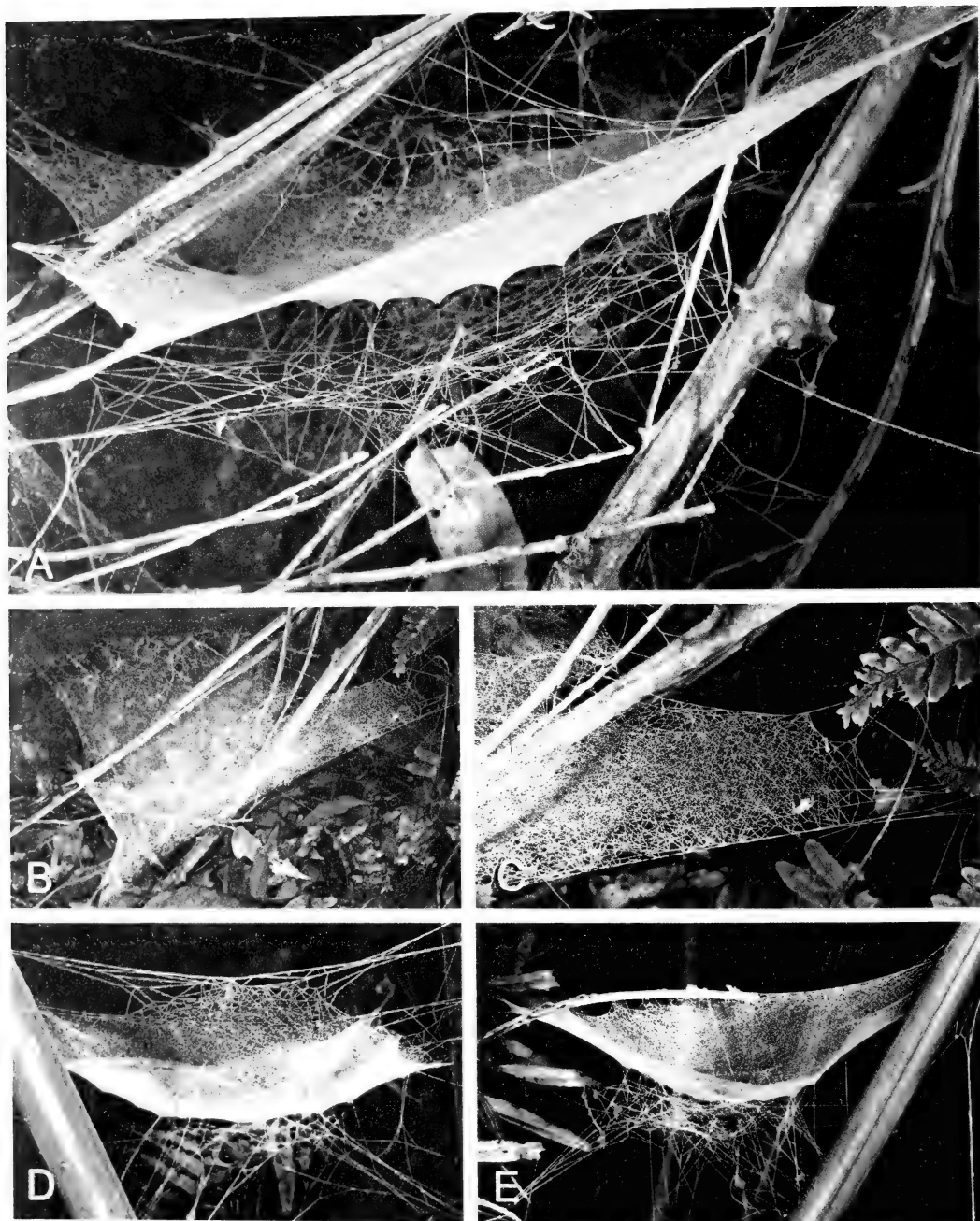


Figure 43. *Laminacauda* webs (8). (A–C) *Laminacauda* sp. ("fPC"), female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0409.NEF, DSC_0405.NEF, DSC_0413.NEF). (D, E) *Laminacauda* sp. ("fChi"), female. Chile, Juan Fernandez Archipelago, Robinson Crusoe Island (DSC_0073.NEF, DSC_0077.NEF).

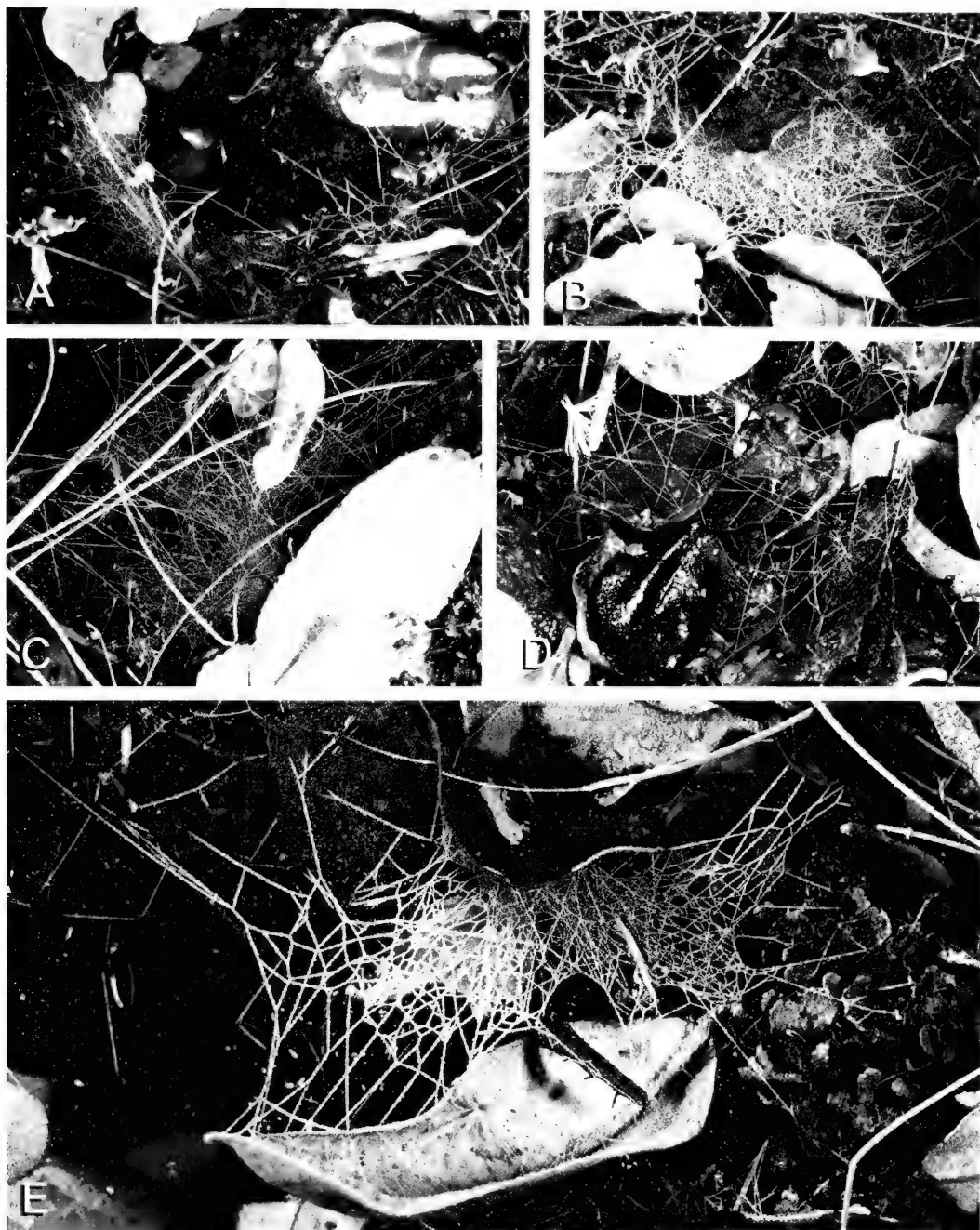


Figure 44. *Laminacauda* webs (9). (A) *Laminacauda parvipalpis* Millidge, 1985, subadult male, female. Chile, Zapallar (DSC_2267.NEF). (B) *Laminacauda parvipalpis*, juvenile (not certain it built this web). Chile, Zapallar (DSC_2270.NEF). (C) *Laminacauda parvipalpis*, female. Chile, Zapallar (DSC_2307.NEF). (D) *Laminacauda parvipalpis*, female. Chile, Zapallar (DSC_2322.NEF). (E) *Laminacauda* sp., juvenile. Chile, Zapallar (DSC_2264.NEF).

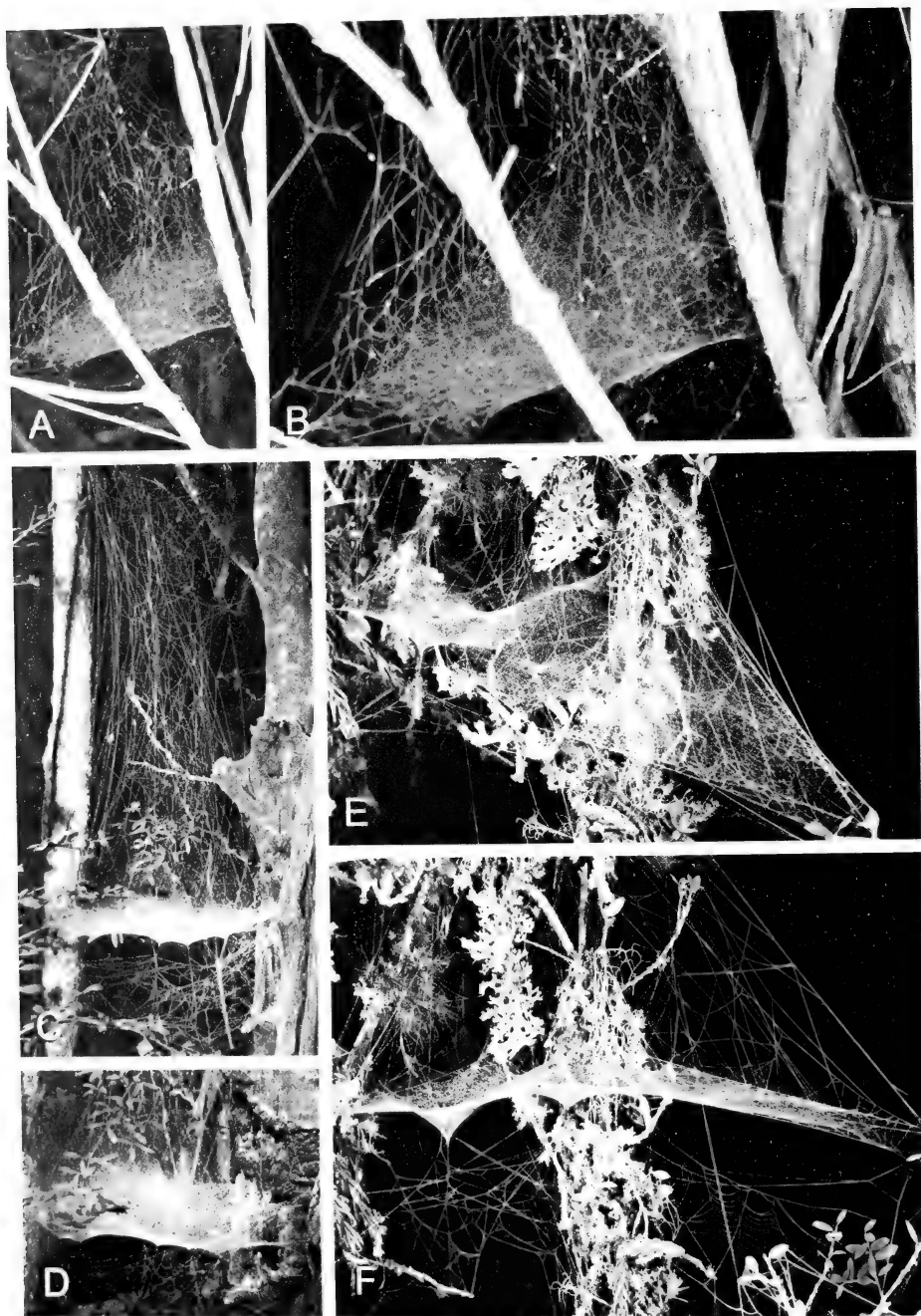


Figure 45. *Laperousea* webs. (A, B) *Laperousea blattifera* (Urquhart, 1887), male. Australia, Queensland, Lamington National Park (GH020417_R03_27_AUS_Laperousea.TIF, GH020417_R03_30_AUS_Laperousea.TIF). (C, D) *Laperousea* sp. (GH02)(GH1677), female. Australia, Victoria (DSC_1292.NEF, DSC_1294.NEF). (E, F) *Laperousea* sp. (GH01), female. Australia, Tasmania, Cradle Mountain National Park (DSC_0257.NEF, DSC_0256.NEF).

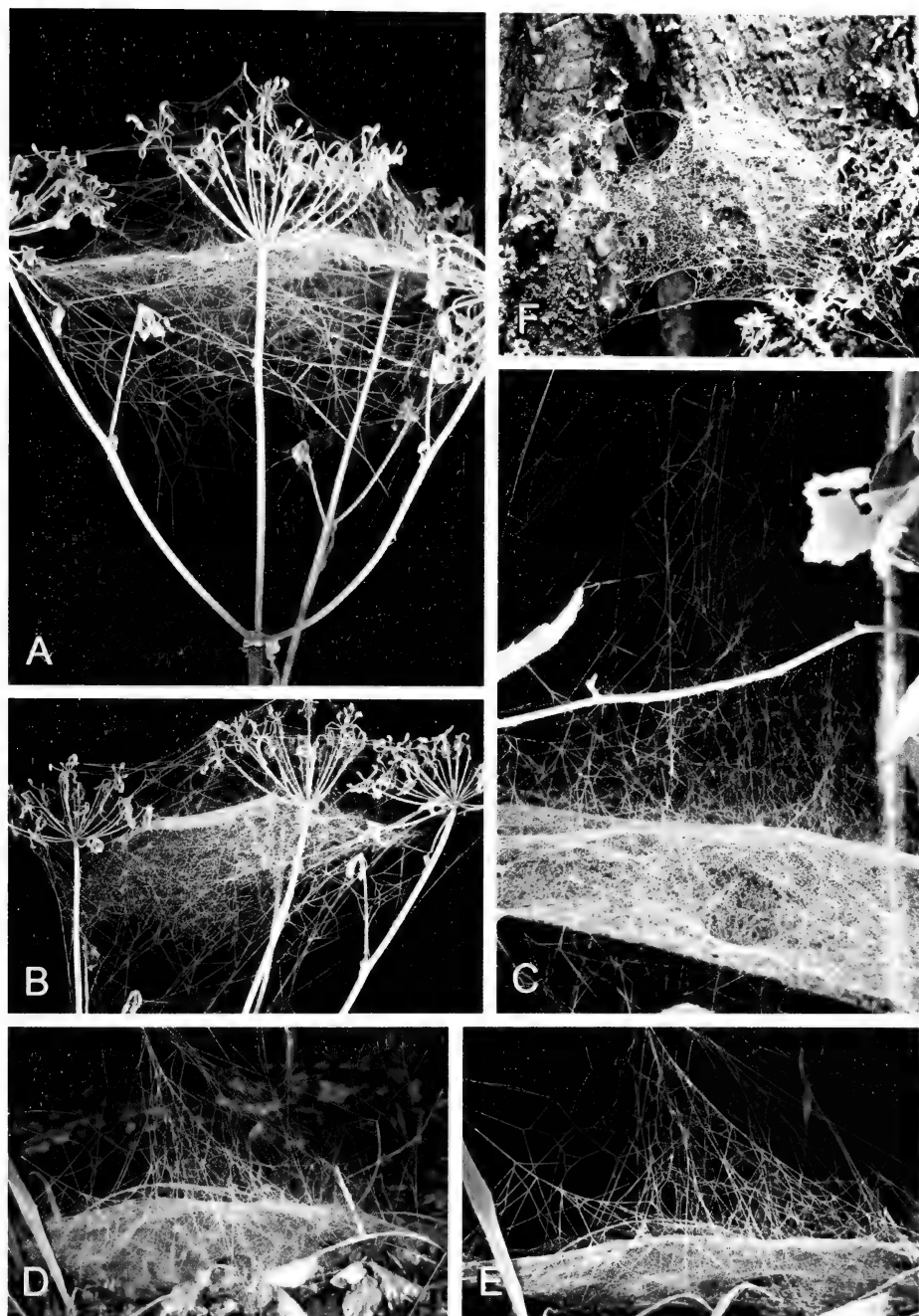


Figure 46. *Linyphia* and *Lepthyphantes* webs. (A, B) *Linyphia triangularis* (Clerck, 1757), female. Sweden, Tullbotorp (GH940815_R00_17_SWE_Linyph_triagul.TIF, GH940815_R00_20_SWE_Linyph_triagul.TIF). (C) *Linyphia triangularis*, female. Sweden, Tullbotorp (GH940815_R00_04_SWE_Linyph_triagul.TIF). (D, E) *Linyphia triangularis*, female. Hestehaven Forest, Denmark (GH940901_R00_20_DEN_Linyph_triagul.tif, GH940901_R00_21_DEN_Linyph_triagul.tif). (F) *Lepthyphantes turatrix* (O. Pickard-Cambridge, 1877), male. USA, Virginia, Jefferson National Forest (DSC_2820.NEF).

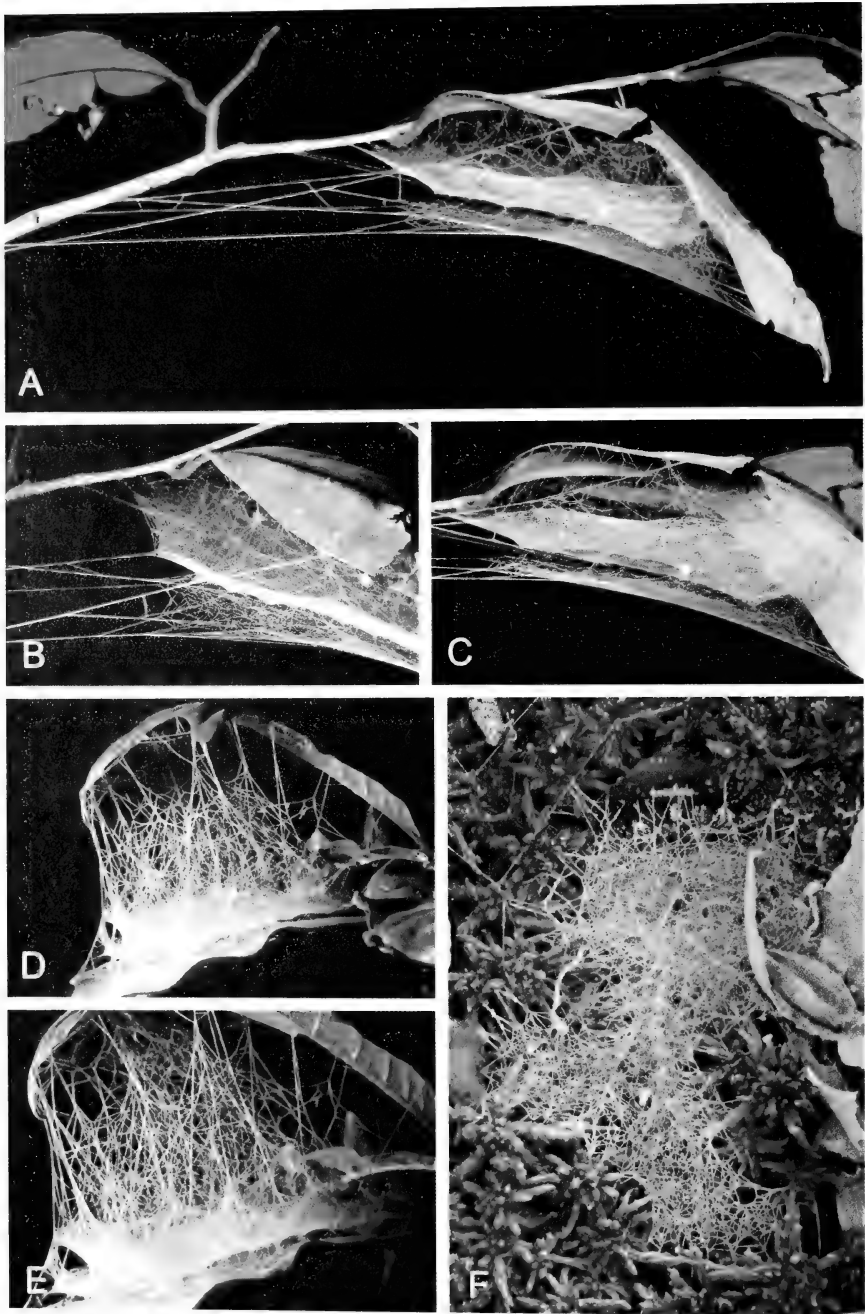


Figure 47. *Mecynidis* and *Mermessus* webs. (A–C) *Mecynidis* sp., female. Cameroon, Mount Cameroon, north of Mapanja (GH920127_R05_25_CAM_Mecyn_sp.TIF, GH920127_R05_20_CAM_Mecyn_sp.TIF, GH920127_R05_26_CAM_Mecyn_sp.TIF). (D–E) *Mecynidis* sp., female. Cameroon, Mount Cameroon, north of Mapanja (GH920127_R06_15_CAM_Mecyn_sp.TIF, GH920127_R06_16_CAM_Mecyn_sp.TIF). (F) *Mermessus tridentatus* (Emerton, 1882), female. USA, Maryland, Patuxent Wildlife Research Center (GH940519_R02_07_USA_Eperig_trident.TIF).

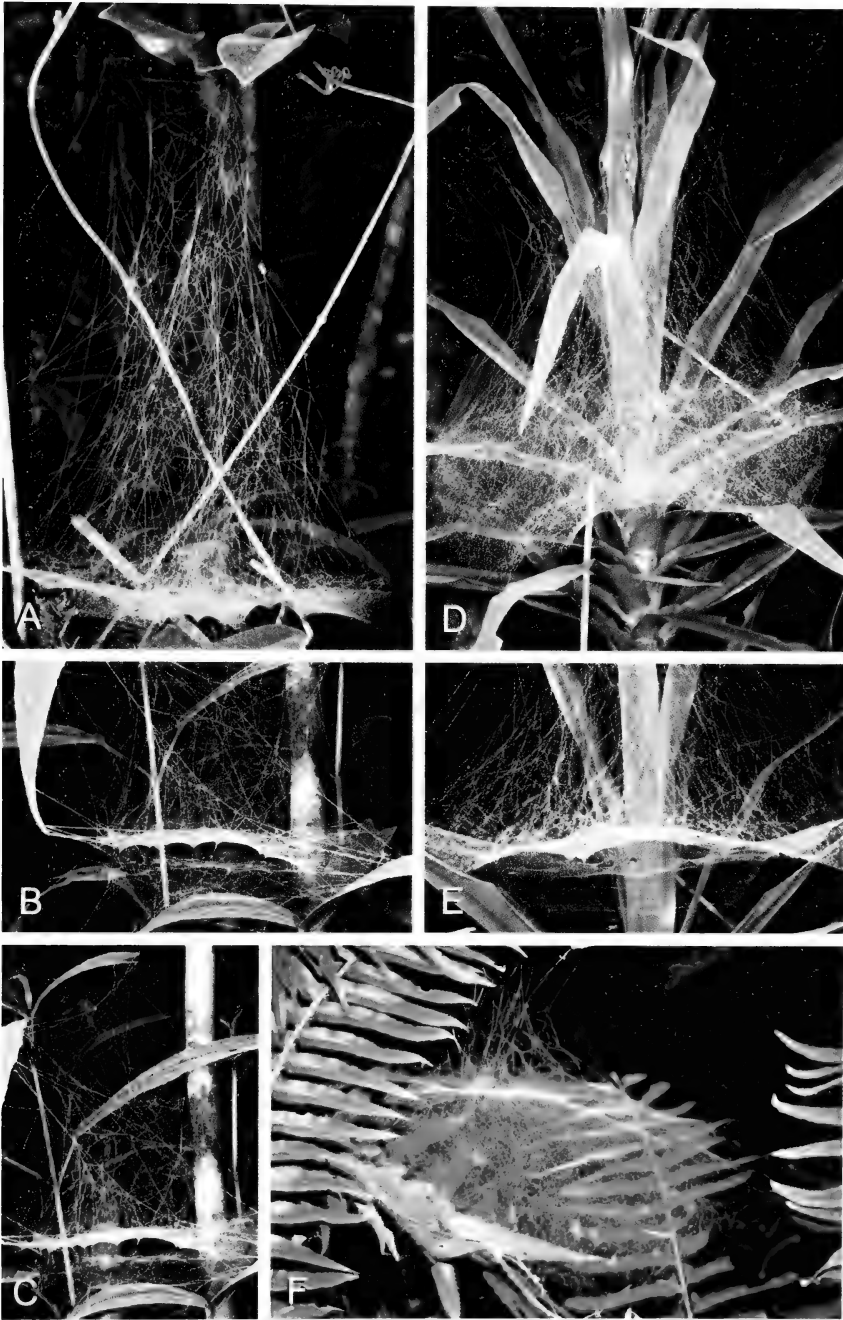


Figure 48. *Microlinyphia* webs. (A) *Microlinyphia simoni* van Helsdingen, 1970, female. Madagascar, Station Forestale Analamazaotra, Mitsinjo (DSC_5990.TIF). (B, C) *Microlinyphia simoni*, female. Madagascar, Station Forestale Analamazaotra, Mitsinjo (DSC_5921.TIF, DSC_5925.TIF). (D, E) *Microlinyphia simoni*, female. Madagascar, Ranomafana (DSC_5449.TIF, DSC_5454.TIF). (F) *Microlinyphia dana* (Chamberlin & Ivie, 1943), female. USA, Washington, Olympic National Park, Elwha River (GH900802_R00_31_USA_Microliny_dana.tif).

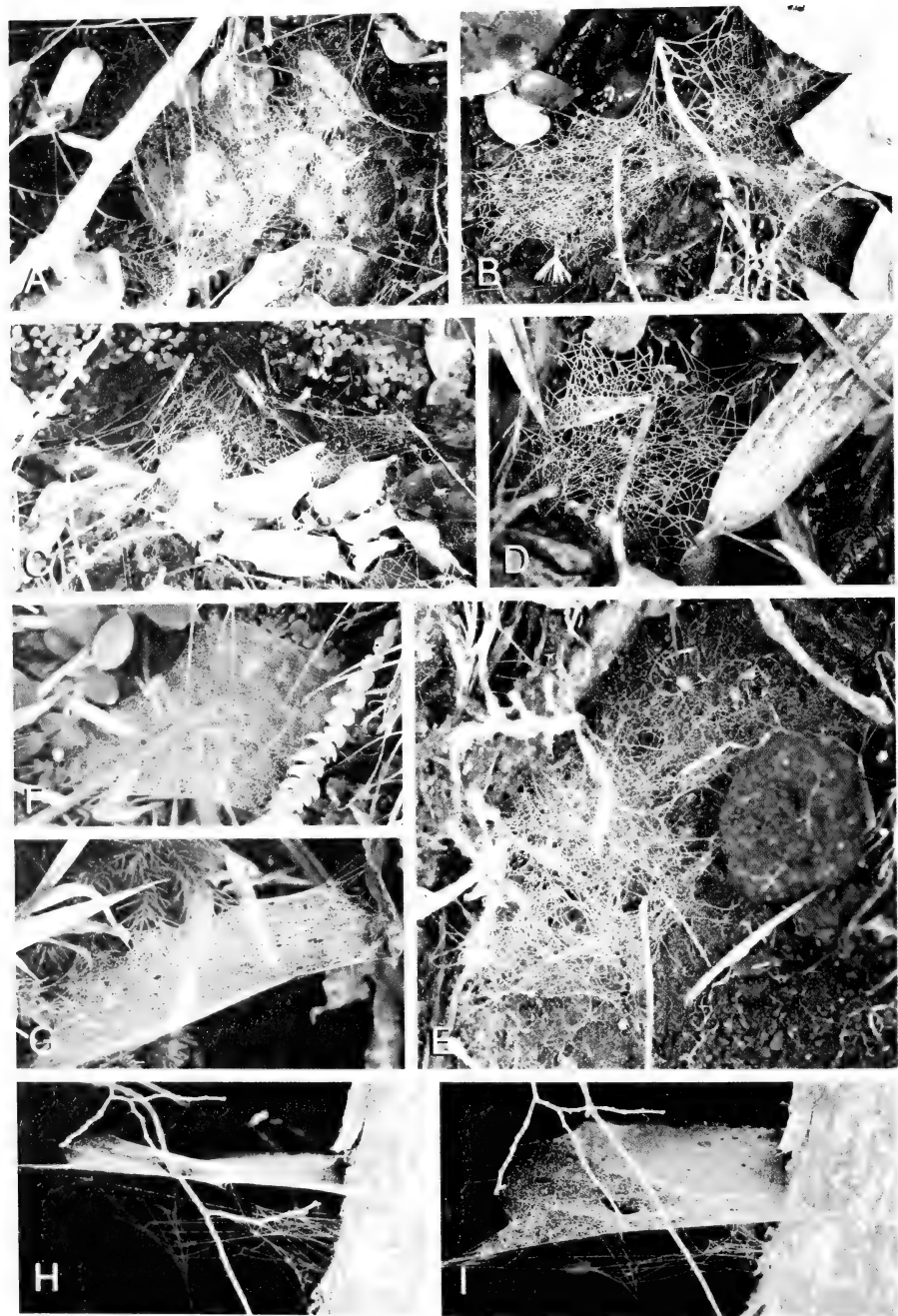


Figure 49. *Neomaso* and *Notholephyphantes* webs. (A–C) *Neomaso pollicatus* (Tullgren, 1901), female. Chile, Zapallar (DSC_2280.NEF, DSC_2298.NEF, DSC_2309.NEF). (D) *Neomaso patagonicus* (Tullgren, 1901), female. Chile, Puyehue National Park (GH001229_R01_31_CHI_Neomaso.tif). (E) *Neomaso* sp., subadult female. Chile, Puyehue National Park (GH001229_R01_31_CHI_Neomaso.tif). (F, G) *Notholephyphantes australis* (Tullgren, 1901), female. Chile, Puyehue National Park (GH001231_R04_21_CHI_Nothelep_austr.TIF, GH001231_R04_19_CHI_Nothelep_austr.TIF). (H, I) *Notholephyphantes australis*, female. Chile, Puyehue National Park (GH010102_R06_12_CHI_Nothelep_austr.TIF, GH010102_R06_13_CHI_Nothelep_austr.TIF).

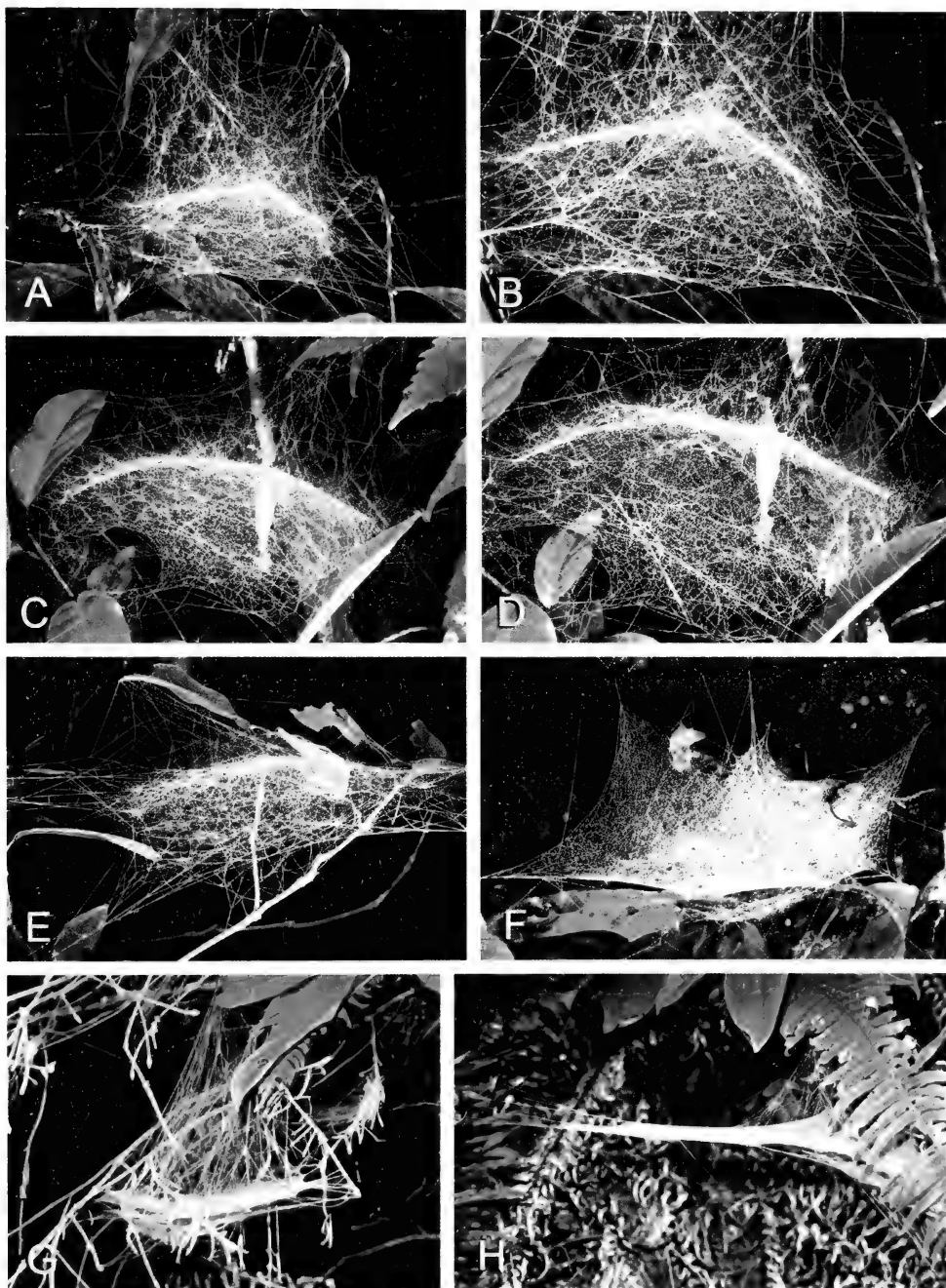


Figure 50. *Neriene* webs (1). (A, B) *Neriene albolimbata* (Karsch, 1879), subadult female. Taiwan, Jianshi Township, Hsinchu County (DSC_1058.NEF, DSC_1059.NEF). (C, D) *Neriene albolimbata*, female. Taiwan, Jianshi Township, Hsinchu County (DSC_1085.NEF, DSC_1093.NEF). (E) *Neriene albolimbata*, female. Taiwan, Jianshi Township, Hsinchu County (DSC_1050.NEF). (F) *Neriene* sp. GH01 (GH1401), male and female. Taiwan, Jianshi Township, Hsinchu County (DSC_1100.NEF). (G) *Neriene digna* (Keyserling, 1886), female. USA, Oregon, Siuslaw National Forest (GH900714_R00_21_USA_Neriene_digna.TIF). (H) *Neriene digna*, female. USA, Oregon, Siuslaw National Forest (GH900714_R00_18_USA_Neriene_digna.TIF).

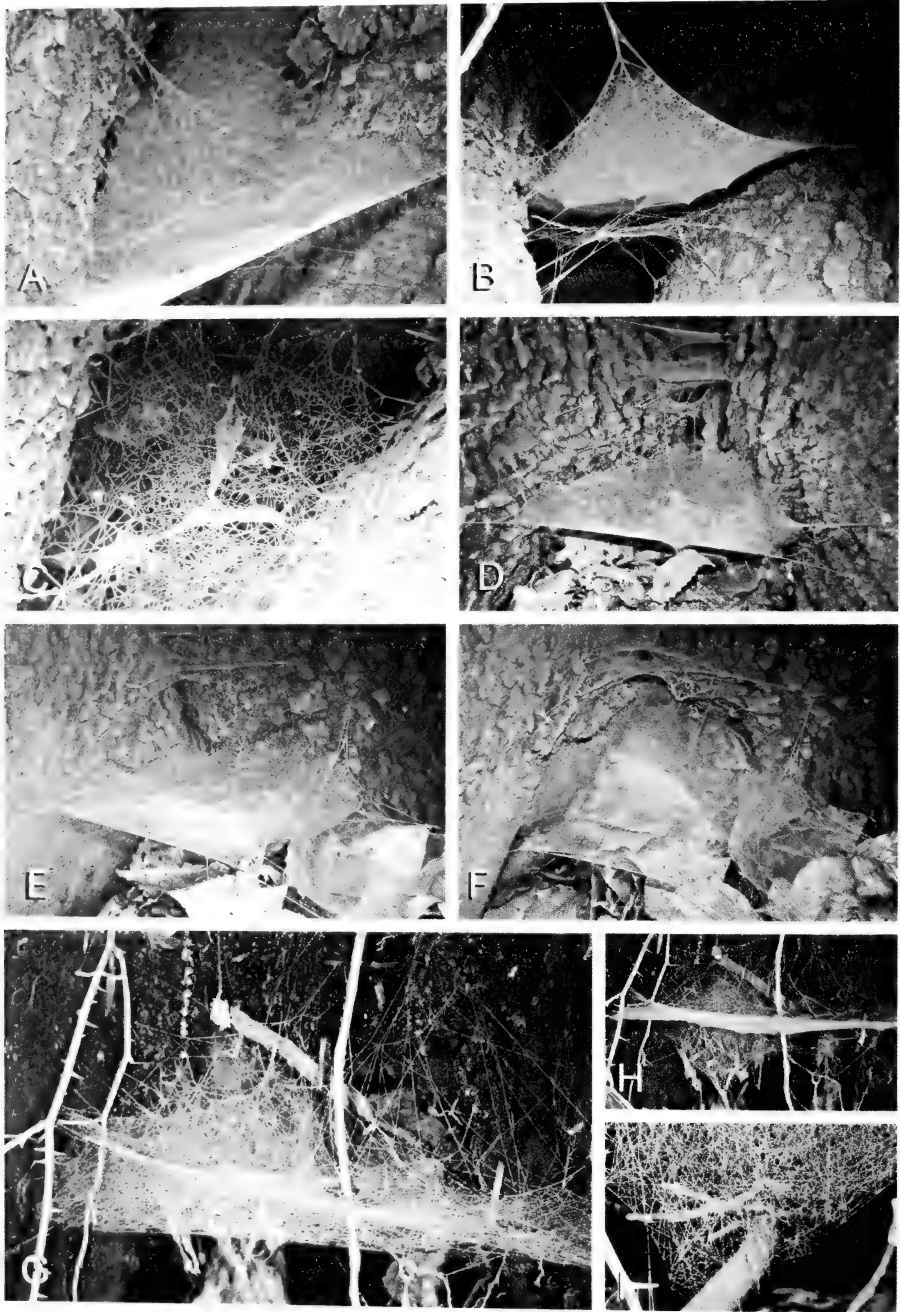


Figure 51. *Neriere webs* (2). (A–C) *Neriere clathrata* (Sundevall, 1830), female. USA, Maryland, Patuxent Wildlife Research Center. (C) Detail of understructure after removal of the main sheet; denser areas are probably remains of an older sheet, suggesting that the understructure already existed (at least, partially) when the new main sheet was built (GH930701_R00_24_USA_Neriere_clathr.TIF, GH930701_R00_26_USA_Neriere_clathr.TIF, GH930701_R00_29_USA_Neriere_clathr.TIF). (D) *Neriere clathrata*, female. USA, Maryland, Patuxent Wildlife Research Center (GH930701_R00_34_USA_Neriere_clathr.TIF). (E, F) *Neriere clathrata*, female. USA, Maryland, Patuxent Wildlife Research Center (GH930701_R00_32_USA_Neriere_clathr.TIF, GH930701_R00_33_USA_Neriere_clathr.TIF). (G–I) *Neriere clathrata*, female. USA, Maryland, Patuxent Wildlife Research Center (GH940510_R00_29_USA_Neriere_clathr.TIF, GH940510_R00_30_USA_Neriere_clathr.TIF, GH940510_R00_34_USA_Neriere_clathr.TIF).

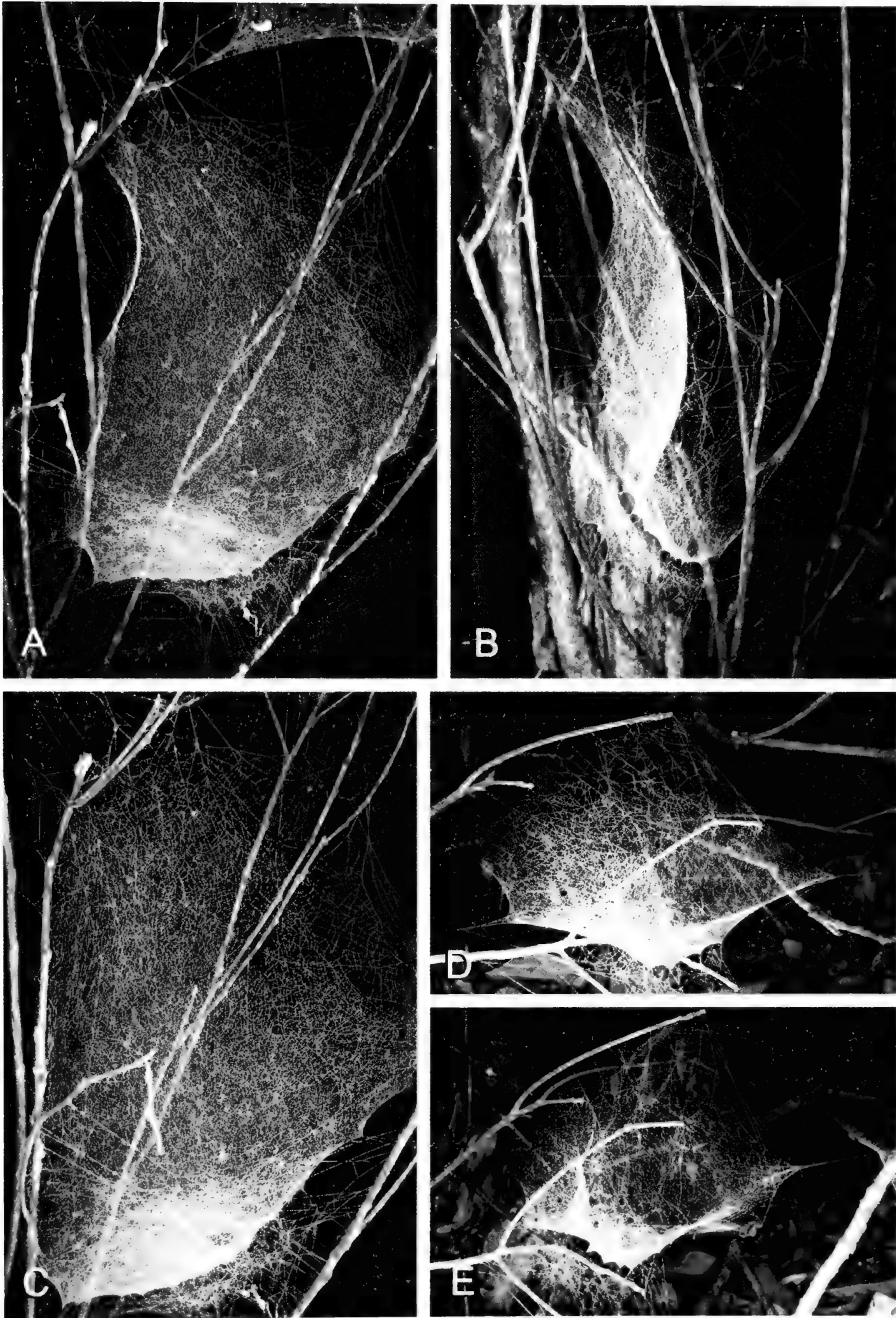


Figure 52. *Neriene* webs (3). (A–C) *Neriene* sp. GH03 (GH1398), female. Taiwan, Jianshi Township, Hsinchu County (DSC_1076.NEF, DSC_1077.NEF, DSC_1081.NEF). The main sheet of this web is vertically oriented. (D, E) *Neriene* sp. GH03 (GH1398), male and female. Taiwan, Jianshi Township, Hsinchu County (DSC_1043.NEF, DSC_1036.NEF).

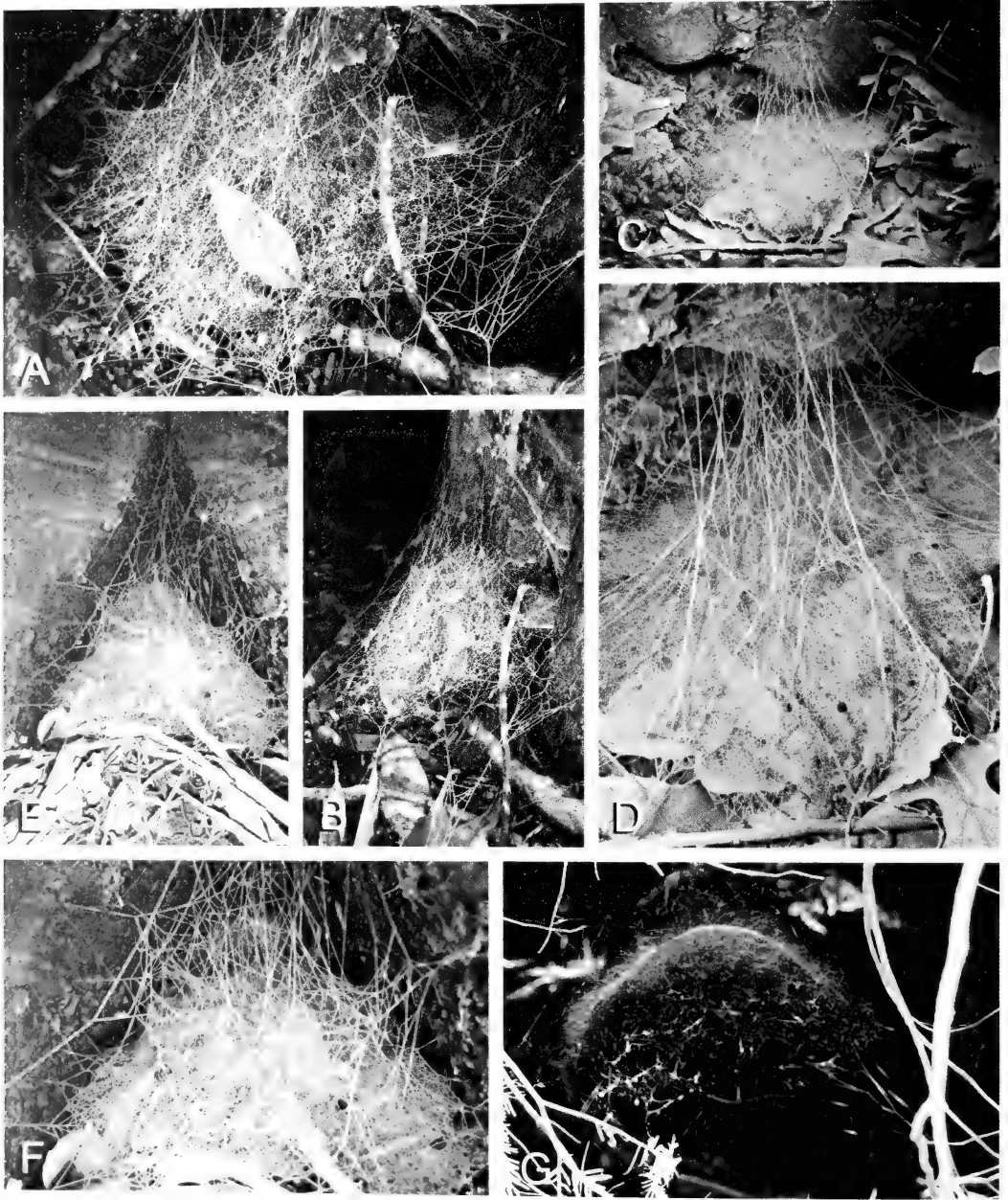


Figure 53. *Neriere* webs (4). (A, B) *Neriere* sp. GH02 (GH1397), female. Taiwan, Jianshi Township, Hsinchu County (DSC 1108.NEF, DSC 1104.NEF). (C, D) *Neriere variabilis* (Banks, 1892), female. USA, Maryland, Patuxent Wildlife Research Center (GH930701_R00_12_USA_Neriere_variab.TIF, GH930701_R00_13_USA_Neriere_variab.TIF). (E, F) *Neriere variabilis*, female. USA, Maryland, Patuxent Wildlife Research Center (GH930629_R00_29_USA_Neriere_variab.TIF, GH930629_R00_33_USA_Neriere_variab.TIF). (G) *Neriere litigiosa* (Keyserling, 1886), female. USA, California, Grizzly Creek Redwoods State Park (GH900718_R00_18_USA_Neriere_litig.TIF).

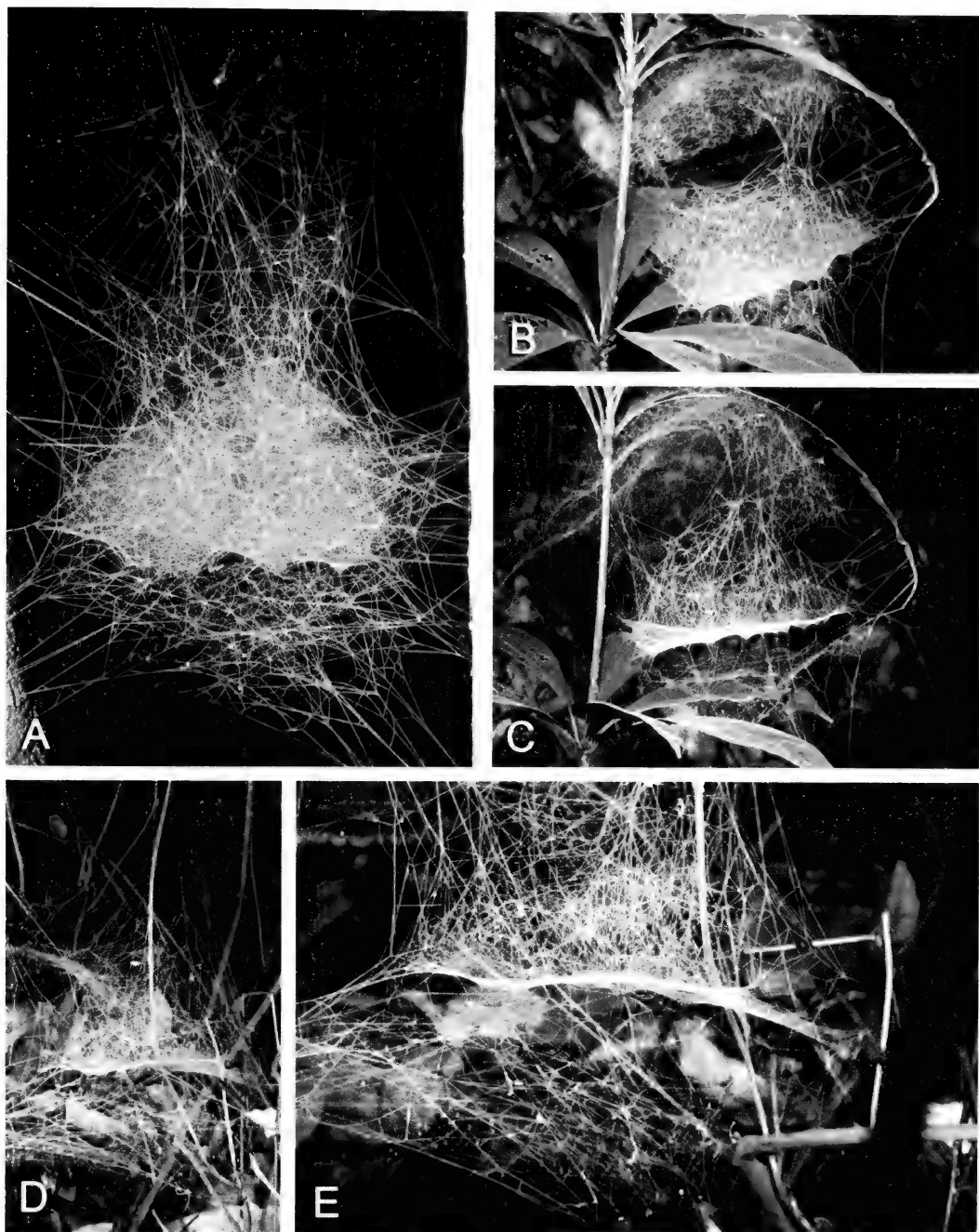


Figure 54. *Neriene* webs (5). (A) *Neriene oxycera* Tu & Li, 2006, male and female. Thailand, Chiang Mai, Doi Chiang Dao (GH031002_R01_14_THA_TIF). (B, C) *Neriene oxycera*, female. Thailand, Chiang Mai, Doi Chiang Dao (GH031002_R01_22_THA_TIF, GH031002_R01_24_THA_TIF) (D, E) *Neriene oxycera*, female. Thailand, Chiang Mai, Doi Chiang Dao (GH031002_R01_28_THA_TIF, GH031002_R01_31_THA_TIF).

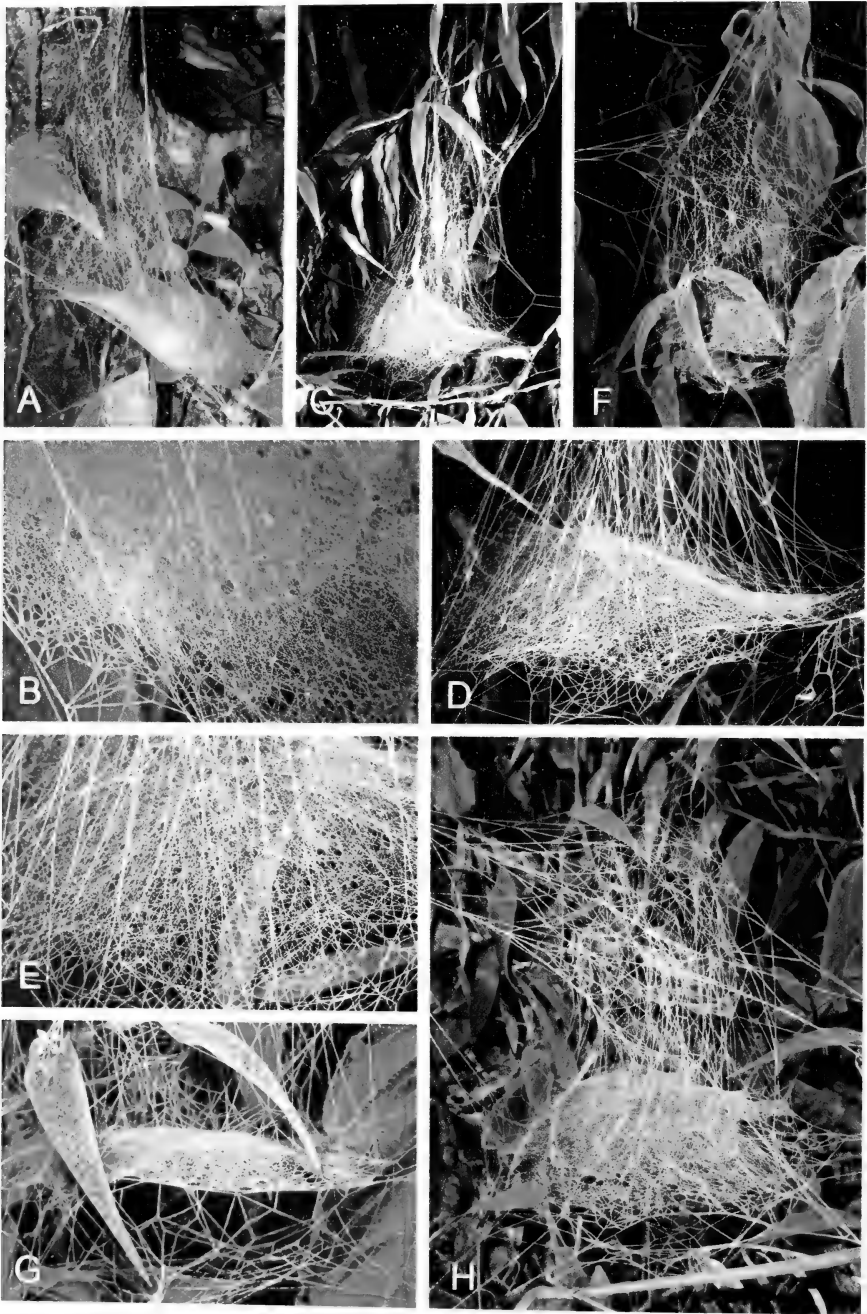


Figure 55. *Neriene* webs (6). (A, B) *Neriene helsdingeni* (Locket, 1968), female. Cameroon, Mount Cameroon, Etome (GH920116_R02_20_CAM_Nereine_helsd.TIF, GH920116_R02_21_CAM_Nereine_helsd.TIF). (C-E) *Neriene helsdingeni*, female. Cameroon, Mount Cameroon, Mann's Spring (GH920123_R03_28_CAM_Nereine_helsd.TIF, GH920123_R03_1_CAM_Nereine_helsd.TIF, GH920123_R03_33_CAM_Nereine_helsd.TIF). (F, G) *Neriene helsdingeni*, female. Cameroon, Mount Cameroon, Mann's Spring (GH920125_R04_22_CAM_Nereine_helsd.TIF, GH920125_R04_23_CAM_Nereine_helsd.TIF, GH920125_R04_22_CAM_Nereine_helsd.TIF). (H) *Neriene helsdingeni*. Cameroon, Mount Cameroon, Mann's Spring (GH920125_R04_25_CAM_Nereine_helsd.TIF).

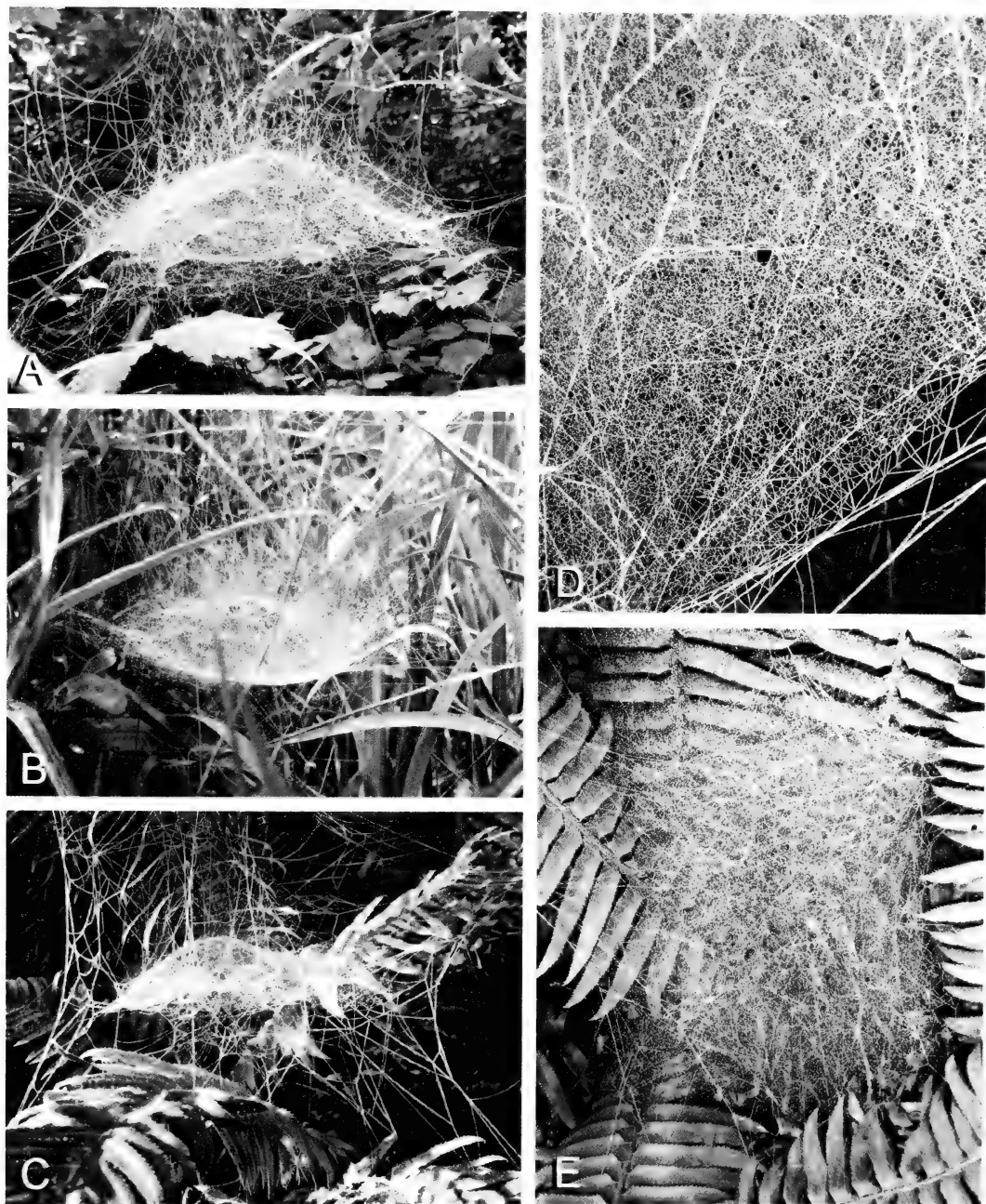


Figure 56. *Neriene* webs (7). (A–E) *Neriene litigiosa* (photos by William G. Eberhard). USA, Washington, Whatcom Co. (A) D#54. (B) D#47. (C, E) D#51. (D) D#53.

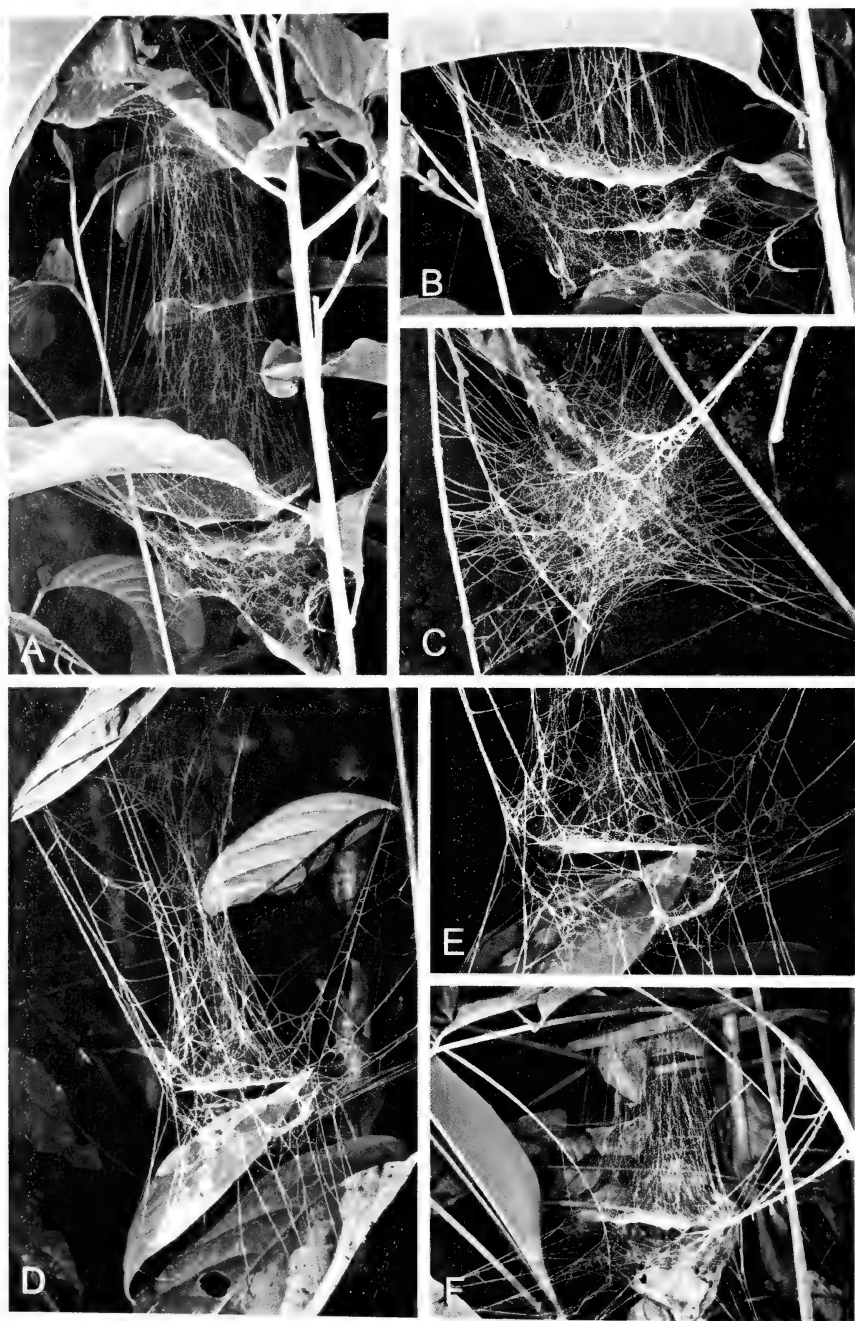


Figure 57. *Novafrontina* webs (1). (A, B) *Novafrontina* sp., female. Brazil, Rio Jufari (DSC_9231.NEF, DSC_9233.NEF). (C) *Novafrontina* sp., female. Brazil, Rio Jufari (DSC_9313.NEF). (D, E) *Novafrontina* sp., female. Brazil, Rio Jufari (DSC_9407.NEF, DSC_9413.NEF). (F) *Novafrontina* sp., female. Brazil, Rio Jufari (DSC_9318.NEF).

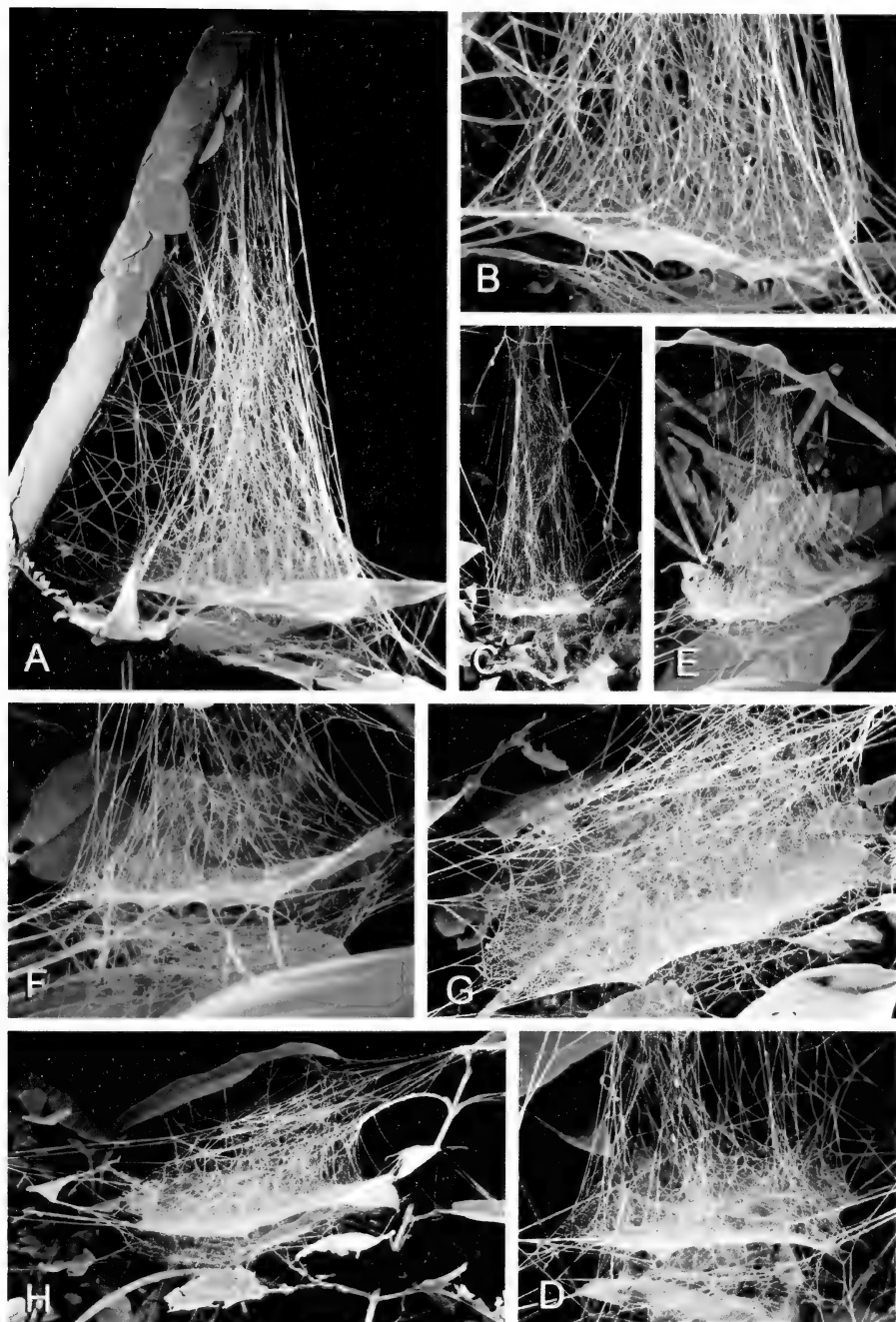


Figure 58. *Novafrontina* webs (2). (A, B) *Novafrontina uncata* (F. O. Pickard-Cambridge, 1902), female. Costa Rica, Estación Biológica La Selva (GH930406_R08_34_CRI_Novafro_uncata.tif, GH930406_R08_35_CRI_Novafro_uncata.tif). (C, D) *Novafrontina uncata*, female. Costa Rica, Sirena, Parque Nacional Corcovado (GH930303_R00_01_CRI_Novafro_uncata.tif, GH930303_R00_15_CRI_Novafro_uncata.tif). (E, F) *Novafrontina uncata*, subadult female. Costa Rica, Estación Biológica La Selva (GH930406_R08_26_CRI_Novafro_uncata.tif, GH930406_R08_31_CRI_Novafro_uncata.tif). (G, H) *Novafrontina uncata*, female. Costa Rica, Sirena, Parque Nacional Corcovado (GH930303_R00_29_CRI_Novafro_uncata.tif, GH930303_R00_23_CRI_Novafro_uncata.tif).

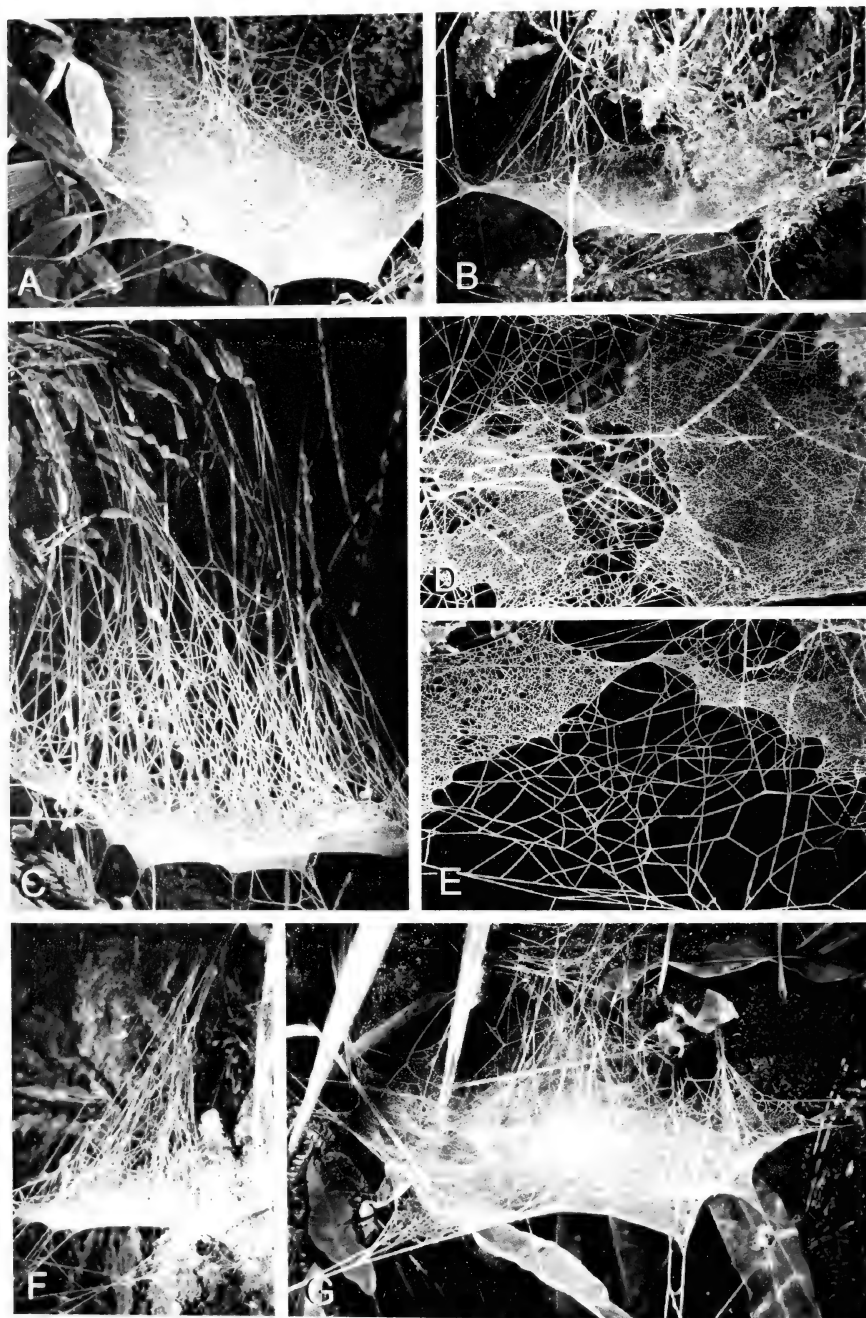


Figure 59. *Orsonwelles* webs (1). (A) *Orsonwelles ambersonorum* Hormiga, 2002, female. Hawaii, Oahu, Mount Tantalus (*Orsonwelles ambersonorum*_F_ow31plates_E.tiff). (B) *Orsonwelles calx* Hormiga, 2002, subadult female. Hawaii, Kauai, Laau Ridge (*Orsonwelles calx*_F_ow32plates_E.tiff). (C) *Orsonwelles falstaffius* Hormiga, 2002, female. Hawaii, East Maui, Waikamoi Preserve (*Orsonwelles falstaffius*_F_ow35plates_E.tiff). (D, E) *Orsonwelles falstaffius* Hormiga, 2002, juvenile, detail of repair work in main platform. Hawaii, East Maui, Waikamoi Preserve (*Orsonwelles falstaffius*_J_ow38plates_E.tiff, *Orsonwelles falstaffius*_J_ow37plates_E.tiff). (F) *Orsonwelles falstaffius* Hormiga, 2002, subadult female. Hawaii, East Maui, Waikamoi Preserve (*Orsonwelles falstaffius*_sF_ow36plates_E.tiff). (G) *Orsonwelles falstaffius* Hormiga, 2002 (no sex information). Hawaii, West Maui, Puu Kukui (*Orsonwelles falstaffius*_X_ow39plates_E.tiff).

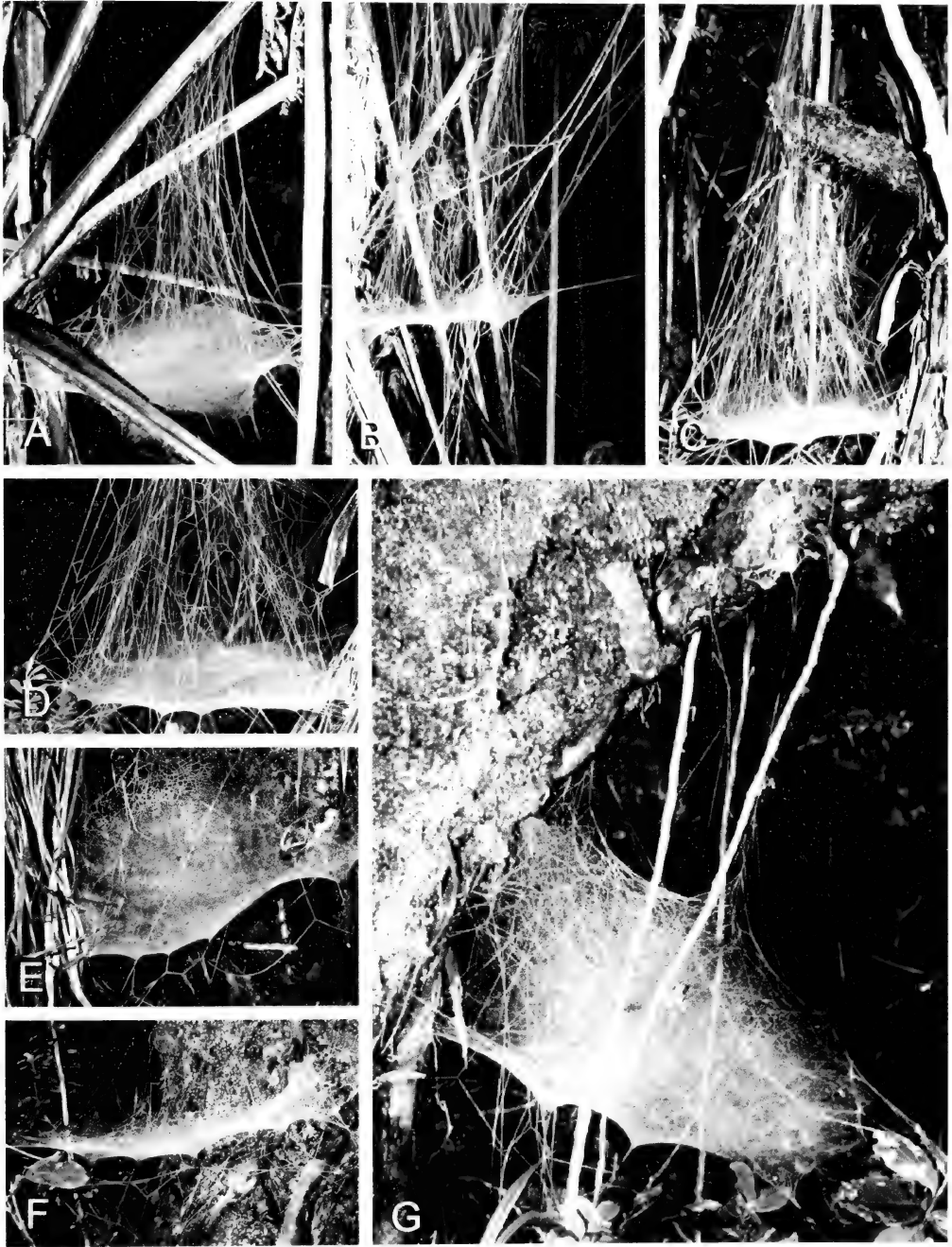


Figure 60. *Orsonwelles* webs (2). (A) *Orsonwelles graphicus* (Simon, 1900), female. Hawaii, Hawaii, Kahaualea Natural Area Reserve (Orsonwelles graphicus_F_ow40plates.tiff). (B) *Orsonwelles graphicus*, female. Hawaii, Hawaii, Pu'u Maka'ala Natural Area Reserve (Orsonwelles graphicus_F_ow41plates.tiff). (C, D) *Orsonwelles graphicus*, female. Hawaii, Hawaii, Pu'u Maka'ala Natural Area Reserve (Orsonwelles graphicus_F_ow42plates.tiff, Orsonwelles graphicus_F_ow43plates.tiff). (E) *Orsonwelles macbeth* Hormiga, 2002, female. Hawaii, Molokai, Kamakou Preserve (Orsonwelles macbeth_F_ow23plates.tiff). (F) *Orsonwelles macbeth*, female. Hawaii, Molokai, Kamakou Preserve (Orsonwelles macbeth_F_ow24plates.tiff). (G) *Orsonwelles macbeth*, female. Hawaii, Molokai, Kamakou Preserve. Runway into retreat is in the upper part of the web (Orsonwelles macbeth_F_ow25plates.tiff).

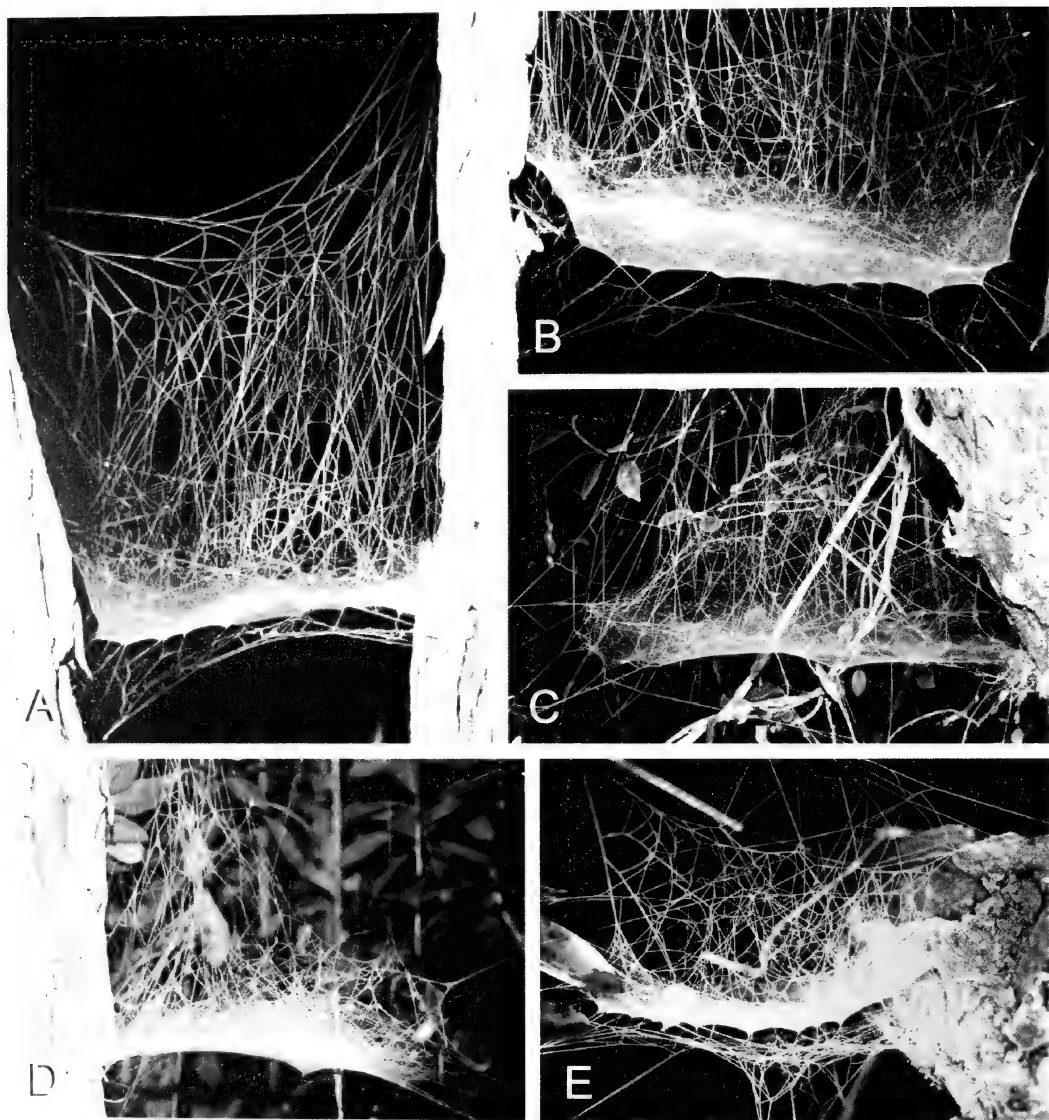


Figure 61. *Orsonwelles* webs (3). (A, B) *Orsonwelles othello* Hormiga, 2002, female. Hawaii, Molokai, Kamakou Preserve (Orsonwelles othello_F_ow34plates.tiff, Orsonwelles othello_F_ow33plates.tiff). (C) *Orsonwelles malus* Hormiga, 2002, female. Hawaii, Kauai, Wai'aleale cabin area (Orsonwelles malus_F_ow20plates.tiff). (D) *Orsonwelles malus*, female. Hawaii, Kauai, Kokee State Park. Runway into retreat is in the bottom left corner (Orsonwelles malus_F_ow22plates.tiff). (E) *Orsonwelles malus*, juvenile. Hawaii, Kauai, Kokee State Park (Orsonwelles malus_J_ow21plates.tiff).

though one was strongly asymmetrical, with one side taller than the others (Figs. 18D, E). The upper tangle of one GH01 web was unusual in being composed largely of more

or less horizontal lines (Figs. 18A, B) but appeared not to be the case in one web of GH02 (Fig. 18F). The upper tangles of all three GH02 webs were more limited to the

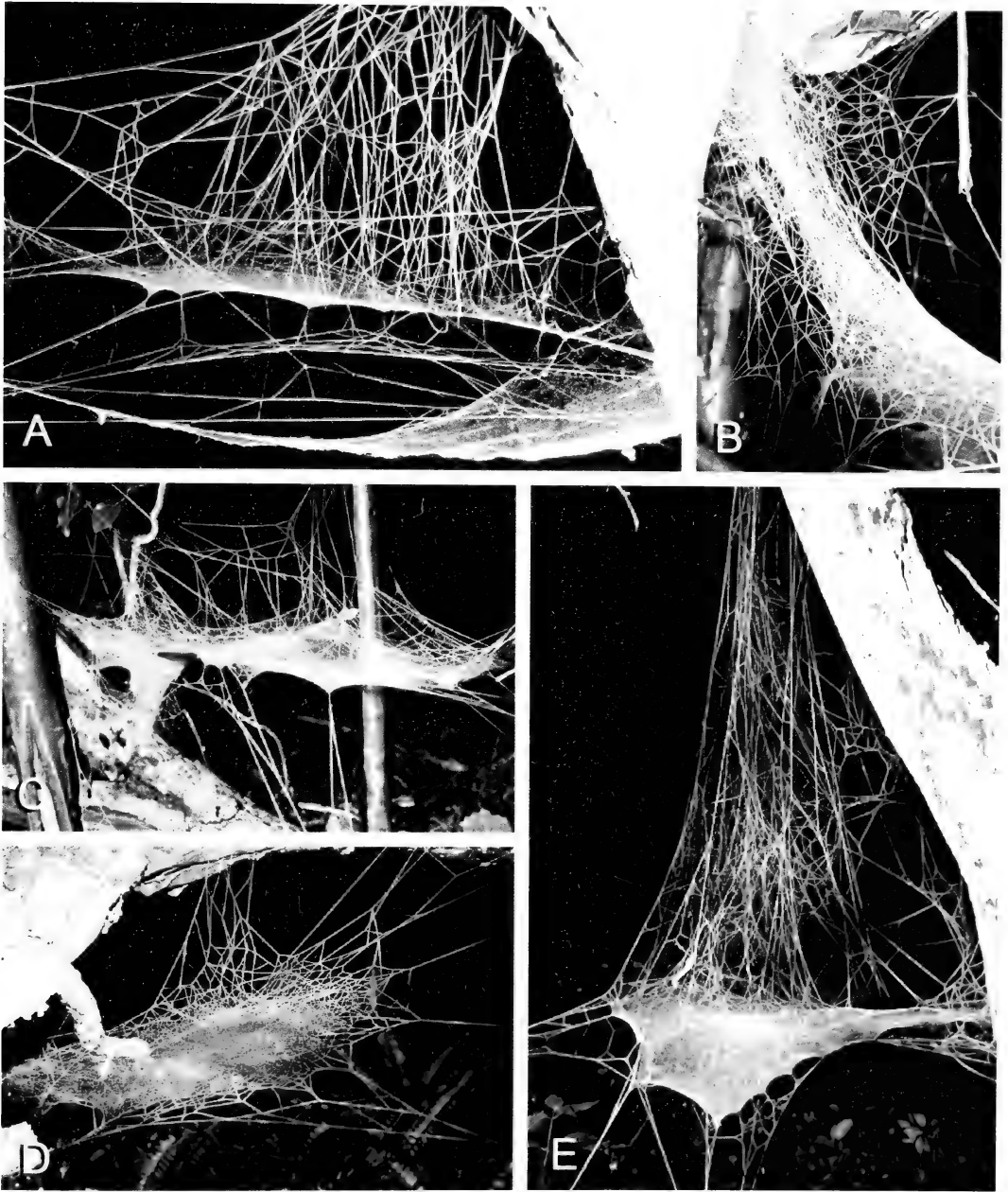


Figure 62. *Orsonwelles* webs (4). (A) *Orsonwelles polites* Hormiga, 2002, juvenile, Hawaii, Oahu, Honouliuli Forest Reserve. Note discarded old sheet at the bottom (*Orsonwelles polites_J_ow27plates.tiff*). (B, C) *Orsonwelles polites*, female, Hawaii, Oahu, Mount Kaala Natural Area Reserve. Detail of funnel (B) (*Orsonwelles polites_F_ow29plates.tiff*, *Orsonwelles polites_F_ow28plates.tiff*). (D) *Orsonwelles polites*, female, Hawaii, Oahu, Wainae Kai (*Orsonwelles polites_F_ow26plates.tiff*). (E) *Orsonwelles polites*, female, Hawaii, Oahu, Palikea (*Orsonwelles polites_F_ow30plates.tiff*).

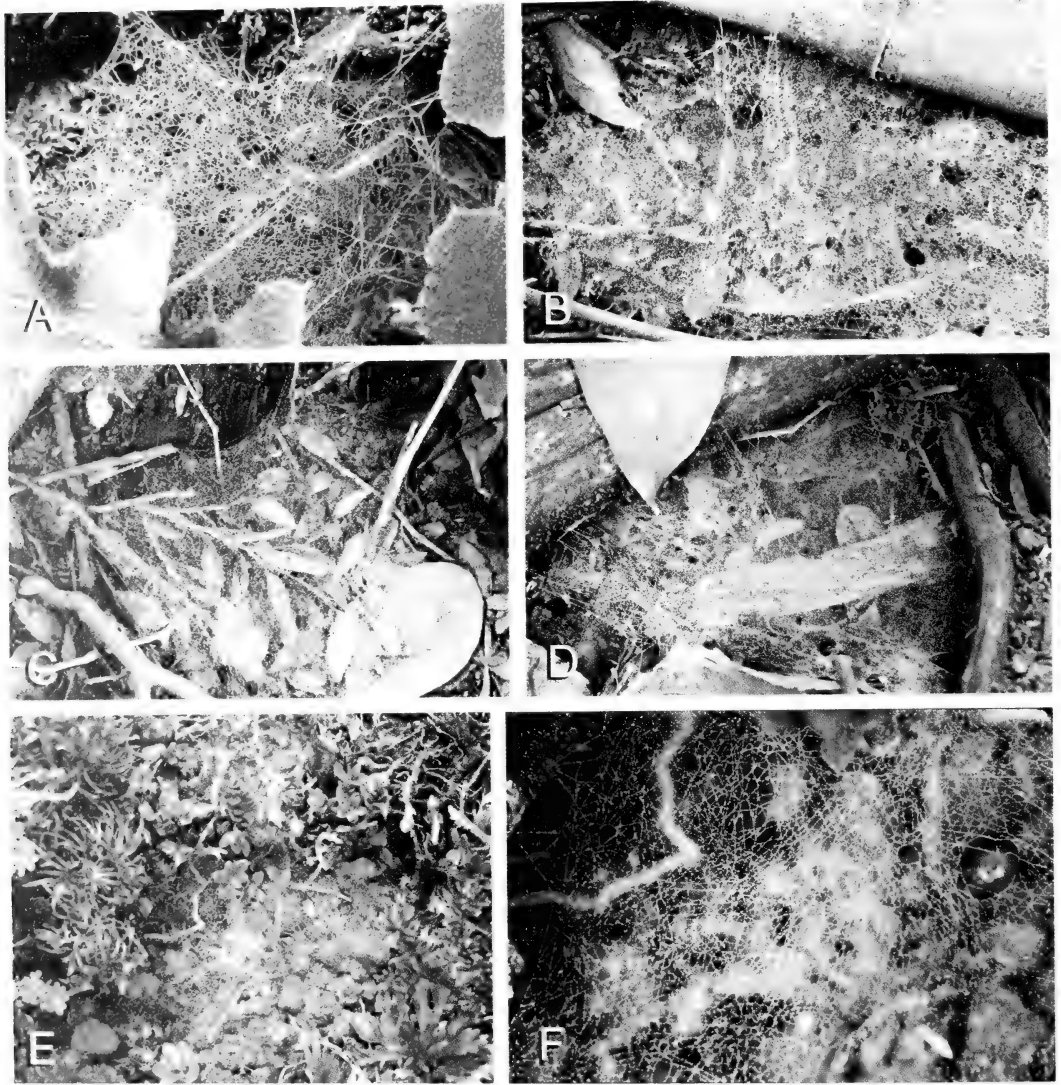


Figure 63. *Ostearius* and *Sphecozone* webs. (A) *Ostearius melanopygius* (O. Pickard-Cambridge, 1880), female with egg sac. Hawaii. Oahu, Palikea (GH990409_R04_05_USA_Ostear_melano.tif). (B) *Sphecozone bicolor* (Nicolet, 1849), female. Chile, Parque Nacional Huerquehue (DSC_2621_ED.NEF). (C, D) *Sphecozone bicolor*, female. Chile, Parque Nacional Huerquehue (DSC_2600_ED.NEF, DSC_2595_ED.NEF). (E, F) *Sphecozone bicolor*, juvenile. Chile, Parque Nacional Puyehue (GH001230_R02_27_CHI_Sphecozone_ED.TIF, GH001230_R02_30_CHI_Sphecozone_ED.TIF).

central area of the sheet; two were low (Figs. 18D, E), and the third was tall, but sparse in the upper part (Fig. 18F).

PUTAOA (ONE SPECIES)

The stemonyphantine genus *Putaoa* includes three described species from Asia.

Three webs of *Putaoa seediq* (Figs. 75A–F), from Taiwan, resembled many linyphiids in having medium-density meshed sheets with only very sparse tangles. The forms of the sheets varied from flat to saddle-shaped (see also Hormiga and Dimitrov, 2017).

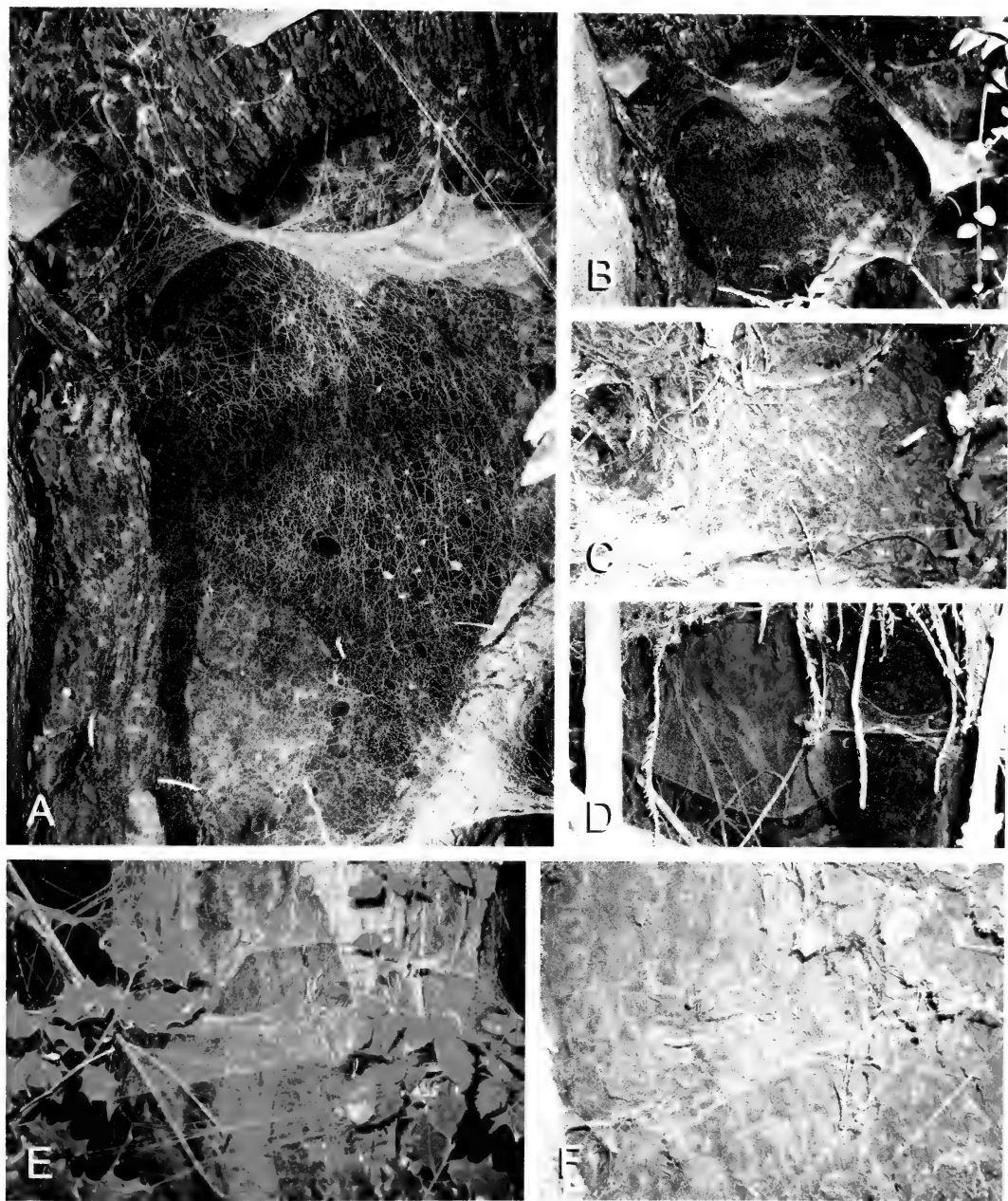


Figure 64. *Pimoa* webs. (A, B) *Pimoa cthulhu* Hormiga, 1994, female. USA, California, Mendocino Woodlands State Park (DSC_5047_ED.NEF, DSC_5057_ED.NEF). (C) *Pimoa cthulhu*, female. USA, California, Mendocino Woodlands State Park (DSC03917_ED.jpg). (D) *Pimoa cthulhu*, female. USA, California, Mendocino Woodlands State Park (DSC03992_ED.jpg). (E) *Pimoa breviata* Chamberlin & Ivie, 1943, female. USA, Oregon, Azalea State Park (GH900716_R00_29_USA_Pimoa_breviata_ED.TIF). (F) *Pimoa breviata*, female. USA, Oregon, Humbug Mountain State Park (DSC03994_ED.JPG).

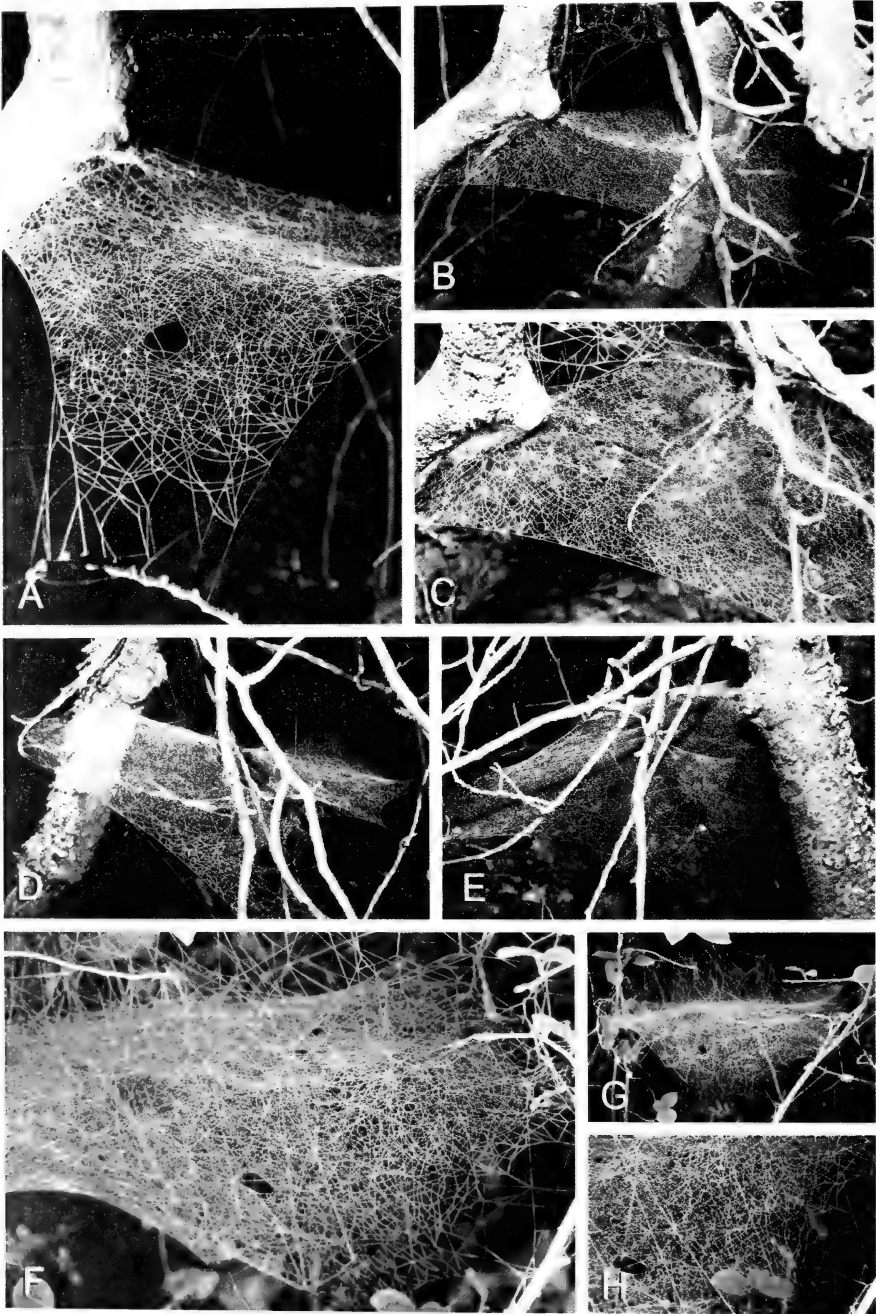


Figure 65. *Pityohyphantes* webs. (A–C) *Pityohyphantes costatus* (Hentz, 1850), juvenile. USA, Virginia, Jefferson National Forest, Mtn Lake Biological Station (DSC_2798.NEF, DSC_2802.NEF, DSC_2796.NEF). (D, E) *Pityohyphantes costatus*, subadult male. USA, Virginia, Jefferson National Forest, Mtn Lake Biological Station (DSC_2807.NEF, DSC_2814.NEF). (F–H) *Pityohyphantes costatus*, female. USA, Maryland, Patuxent Wildlife Research Center (GH940510_R00_02_USA_Pityohy_cost.TIF, GH940510_R00_09_USA_Pityohy_cost.TIF, GH940510_R00_04_USA_Pityohy_cost.TIF).

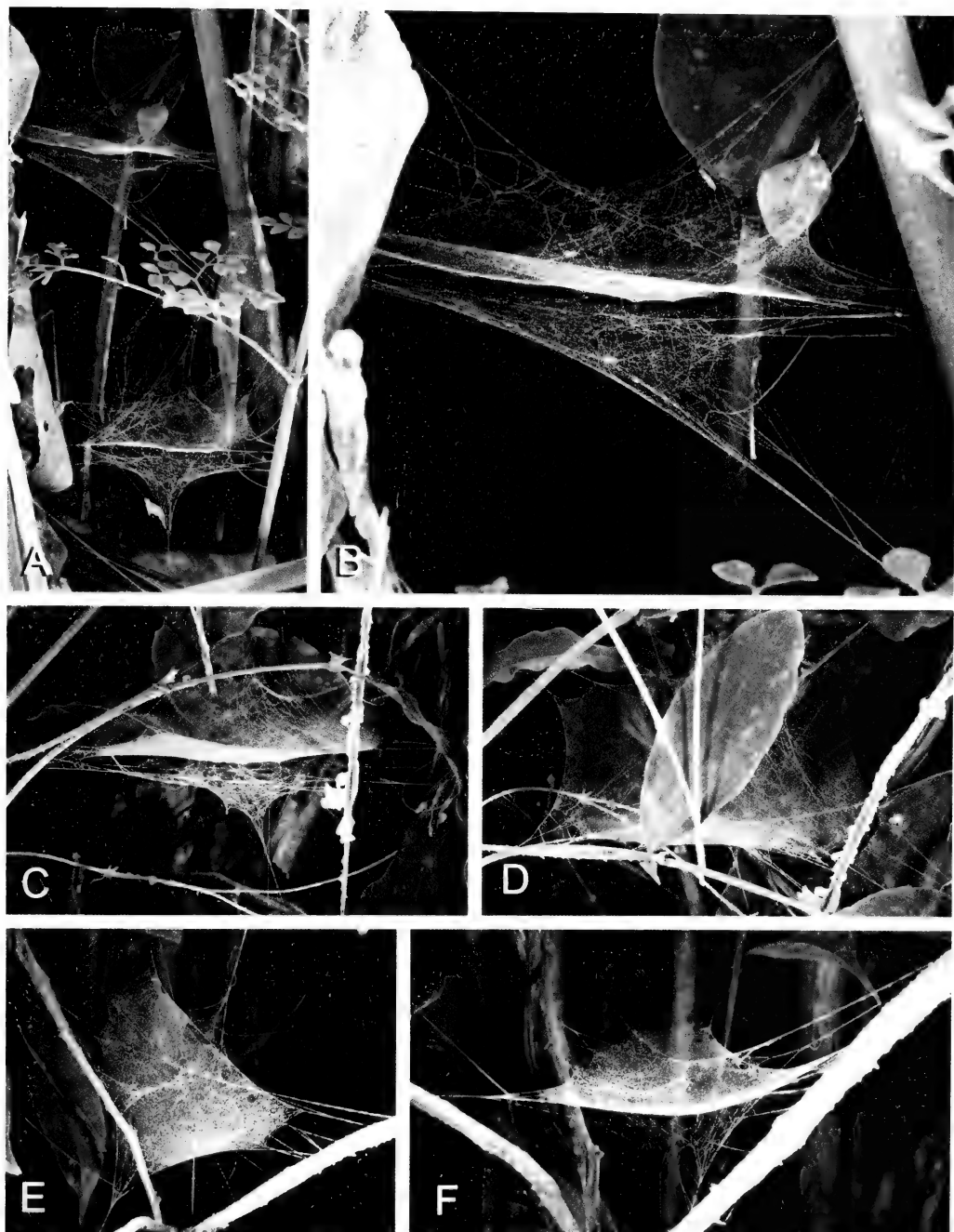


Figure 66. *Pocobletus* webs (1). (A, B) *Pocobletus* sp. GH32, subadult male. Brazil, Rio Jufari (DSC_9240.NEF, DSC_9237.NEF). (C, D) *Pocobletus* sp. GH32, female. Brazil, Rio Jufari (DSC_9278.NEF, DSC_9280.NEF). (E, F) *Pocobletus* sp. GH32, subadult male. Brazil, Rio Jufari (DSC_9287.NEF, DSC_9288.NEF).

They all differed from all known linyphiid webs in having a cylindrical retreat either at one edge of the sheet (Figs. 75A, B, E, F) or above it (Figs. 75C, D). A close relative, *Stemonyphantes lineatus*, is also known to build a retreat “at one side of the web” (van Helsdingen, 1968: 138).

Pimoidae

Moderate Intrageneric Diversity. *PIMOA* (WEBS OF TWO SPECIES). The genus *Pimoa* groups about 80 described species from eastern North America, southern Europe, and Asia. The photographed webs of both of the North American *Pimoa* species were elevated. The three webs of *P. cthulhu* (Figs. 64A–D), from California, differed from all known linyphiid webs. They were built against vertical walls in large cavities (e.g., at the base of a tree trunk) and had an extensive planar vertical sheet parallel to this surface that seemed, at least in one web (Figs. 64A, B), to be a continuation of the top of a vaguely saddle-shaped sheet. In at least one (Fig. 64C) and perhaps another (Figs. 64A, B) was a tubular retreat near the top. Two webs of the American *Pimoa breviata* Chamberlin & Ivie, 1943 (Figs. 64E, F), varied substantially. One was a sparsely meshed, possibly weakly dome-shaped sheet with little or no tangle above or below and was also built against a vertical tree trunk. The spider rested near the trunk with no perceptible retreat in one case (Fig. 64F); the second web (Fig. 64E), also against a tree trunk and with little or no tangle, had a more extensive sheet with a denser mesh and a retreat under the tree bark; other webs of *P. breviata* in the same area also had retreats. Hormiga (1994a: figs. 5, 6) depicts an additional web of *P. breviata*, a horizontal sheet with a relatively open mesh. European species of *Pimoa* usually inhabit the outermost section of caves where they can be found on cave walls or among large rocks on the ground, hanging on horizontal

sheet webs (Isaia et al. 2011; Mammola et al., 2016).

Summary of Intrageneric Variation: Rampant Divergence

In sum, the data from the present study and from previous publications present a clear pattern: there is frequent substantial variation among the webs of congeneric (i.e., closely related) species. This pattern is clear even though present coverage is only fragmentary (two-thirds of the 21 genera we reviewed above were represented by only two to three species), and incomplete coverage undoubtedly results in a bias to underestimate the diversity of web forms.

Several additional factors also indicated that current knowledge seriously underestimates the diversity of linyphiid webs. In the first place, the taxonomic coverage in the family is only fragmentary. Counting the >60 species represented here, combined with previously published web photos from just under 30 other species, web forms have been documented in just under 2% of the known linyphioid species (and this is an overestimate because it ignores the many species not yet described). At the level of genera, the present paper adds information on 26 genera; combined with the published web photos for approximately 12 other genera; this represents a total of only about 6% of the 625 genera in Linyphiidae and the two genera in Pimoidae. This lack of taxonomic coverage, in combination with the high diversity of web forms even within a single genus and the consistently overly typological nature of current knowledge of linyphiid web designs, suggests that a great deal of diversity is yet to be discovered.

It seems likely, nevertheless, that there are phylogenetic signals in the intrageneric differences. For example, the genus *Neriene*, for which we have web information on the greatest number of species (17 of 60 described species), there seems to be one group with elevated, deep, cup-like sheets;

another group with elevated, pronounced, dome-shaped sheets; and one species with a flat web near the ground. It remains to be determined, of course, whether these represent natural groups of species.

There are several suggestions for possible convergences in different genera. The vertical trunk sheets in the erigonine *Laminacauda rubens* were similar to those of the distantly related “micronetine” *Obscuriphantes obscurus* (Blackwall, 1841) which built dense vertical sheets against tree trunks (Nielsen, 1932: fig. 410). The *O. obscurus* webs differed, however: the upper edge curved toward the trunk where it was broadly attached; long, straight lines anchored the sheet to branches above and below; and the spider rested facing downward on the trunk and holding the sheet with its hind tarsi (the spider dropped readily when disturbed) (Nielsen, 1932). Vertical sheets are also built against tree trunks by *Drapetisca socialis* but are relatively much smaller and probably function mostly as trip lines to alert the spider to the presence of prey (Schütt, 1995). The asymmetrical, vertical sheets formed by the upward extension of one upper wall of a cup in *Neriene* GH03 (Figs. 52A, B) resembled the downward extension of the lower wall of a dome in the distantly related *Putaoa seediq* (Figs. 75C–F). The slime on sheets of *Tapinopa* spp. resembled that on *Laminacauda magna* webs. (However, although slime seems to be a typical feature in the former species, it is only occasionally found in the latter.) The pattern of intrageneric diversity we have found in linyphioids resembles that in the webs of another large araneoid family, Theridiidae (Eberhard et al., 2008).

Our sample of Pimoidae is too small to justify strong conclusions, but there are hints of the same combination of intrageneric diversity and convergence in *Pimoida*; *P. cthulhu* also had a downward extension of the lower wall of a dome (Fig. 64C). No webs are known in *Nanoa enana* (Hormiga

et al., 2005), the single species of the only other pimoid genus.

The fragmentary nature of the data on webs, along with the lack of a well-supported phylogeny of the family Linyphiidae (but see Fig. 2 and Arnedo et al., 2009; Wang et al., 2015; Silva-Moreira et al., in prep.), have discouraged us from attempting to trace web evolution within Linyphiidae on a phylogenetic tree. A well-supported outline of their phylogeny will be crucial in classifying linyphioid webs and grouping them in biologically realistic ways and to trace the evolutionary changes in web architecture.

Intraspecific Variation

Web traits showed substantial intraspecific variation (with coefficients of variation ranging up to >90%) in two linyphiids, *Diplothyron simplicatus* and *Neriene coosa* (Eberhard, 2022). The variables included the symmetry and curvature of the dome-shaped sheet, the sheet's orientation with respect to horizontal, and relative sizes of the tangles compared with the diameter of the sheet. Suter (1984) also found substantial variation in the curvatures of the cups of *Frontinella pyramitela*. Alderweireldt (1994) linked substantial variation in the size of *Bathypantes gracilis* (Blackwall, 1841) webs to the sizes of available spaces in which to build in cultivated fields. Despite the relatively small samples in the present study, several examples were of significant intraspecific variation.

Two *Pityohyphantes costatus* webs were nearly naked, open-meshed sheets that sloped up to a sheltering object on one side where the spider rested (Figs. 65A–C); in contrast, a third web had a weakly dome-shaped sheet with no sheltering object and a medium-dense upper tangle (Figs. 65F, G). One of these webs had numerous V-shaped lines at one edge of the sheet (Figs. 65A, C), but another web lacked them (Fig. 65F). In one web of *Mecynidis* sp. the lower

tangle formed a clear sheet (Figs. 47A–C), but in another the principal sheet was just above a large leaf, with only a few lines and no sign of a sheet in the lower tangle (Figs. 47D, E). In *Novafrontina uncata* the relative height of the upper tangle varied from about 0.5 to three sheet diameters (Figs. 58A, H). The form of the sheet of *Putaoa seediq* varied from sharply dome-shaped or conical (Figs. 75C, D) to quite flat (Fig. 75A). *Laminacauda magna* may have varied in the presence or absence of a second “sandwich” sheet (Fig. 41D). Even a single web sometimes provided variations, as in the *Walckenaeria* sp. web with long frames with many “V” attachments of sheet lines along with one elevated edge that lacked clear frame lines and had long anchor lines instead (Fig. 77E). Undoubtedly much further intraspecific variation remains to be documented.

In sum, it is probable that linyphiid webs usually show substantial intraspecific variation in a number of traits, which implies that the small samples of webs for the species in this study (as well as the web descriptions throughout the published literature) likely underestimate of the diversity of webs built by any single species. This observation, in turn, implies that the high degree of intrageneric diversity described above is probably a substantial underestimation.

Some of this intraspecific variation probably represents adjustments to the environment rather than imprecision. For instance, the *N. uncata* web with an especially low upper tangle (compare Figs. 58G, H with 58A–E) was built at a site where there were no potential attachment sites higher above the sheet. Thus, some differences in web design probably resulted from variation in web site choices by the spiders. Nothing is known concerning how linyphioid spiders explore and choose web sites. Benjamin and Zschokke (2004: 122) mentioned that *Linyphia hortensis*, which built naked sheets, performed a “short exploratory stage with

the spider moving in a space where the web was later built,” but gave no further details. Repairs and additions of lines to webs on subsequent nights, which have been documented in *Drapetisca socialis* (Schütt, 1995), *Linyphia triangularis* (Benjamin et al., 2002), and *Diplothyron simplicatus* and *Neriene coosa* (Eberhard, 2022), probably add further intraspecific variation. The almost complete absence of webs in this study that had stems and leaves projecting through them (the only clear exceptions are *Neriene coosa* [Eberhard, 2022] and *Linyphia hortensis* [Nielsen, 1932]) implies that exploratory behavior by linyphioids before web construction must inform the spider regarding the sizes of open spaces in which to build.

The Evolutionary Derivations and Convergences Involving Linyphioid Webs

Recent phylogenomic analyses (Kulkarni et al., 2021: fig. 4) suggest that Linyphiidae and Pimoidae form a clade with Cyatholipidae (but see Kallal et al., 2021). Few studies have documented cyatholipid webs, but all available data and our own observations indicate that they build horizontal sheet webs. Griswold (1987: 500) mentions that cyatholipids build “small horizontal sheet webs”, and Davies (1978: 293) described the web of *Teemenaarus* as a “filmy sheet web against the bark of forest trees.” Our own observations of cyatholipids webs in the genera *Alaranea*, *Forstera*, *Matilda*, *Teemenaarus*, *Tekella*, *Tekelloides*, and *Wanzia* agree (Figs. 3–7) that they all built densely meshed, naked or nearly naked horizontal sheets in forests, usually above the ground on vegetation and against tree trunks. These genera have triads on their posterior lateral spinnerets, implying that at least some lines in their webs are sticky. They also have reduced numbers of aciniform spigots (Griswold, 2001), implying that they do not attack prey by wrapping them. The major difference of the webs of

these small to very small spiders compared with linyphioids is their combination of a lack of tangles and elevated web sites. They share with linyphiids the relatively long and thin legs (Griswold, 2001; Jocqué and Dippenaar-Schoeman, 2007) but have only short medium paturons.

The preliminary suggestion is thus that the most recent common ancestor of linyphiids, pimoids, and cyatholipids built sheet webs. These three families may be closely related to physoglenids, which also build elevated horizontal sheets, with more or less sparse tangles (Figs. 8–10); at least some also have triads (G. Hormiga, unpublished) (also implying sticky silk in their webs) and relatively long, thin legs (Forster et al. 1990), and at least some have reduced aciniform spigots (data are incomplete), implying that they do not attack prey by wrapping them.

Farther back in time, linyphioids, cyatholipids, and physoglenids are thought to be derived from an orb-weaving ancestor (Kulkarni et al., 2021). The typical predatory strategy of orb weavers differs in basic ways from that of these sheet weavers: orb weavers employ relatively low numbers of strong lines that bear relatively large amounts of adhesive and that are placed in precise locations with respect to one another; in contrast, the linyphiids (and probably also their allies) rely on much larger numbers of relatively fine lines that bear much smaller droplets of adhesive and that are placed in much less consistent patterns with respect to each other.

Additionally, linyphiids differ from many orb weavers in making extremely rapid attacks on prey. Some orb weavers, such as the tetragnathid *Leucauge mariana* (Taczanowski, 1881) (Briceño and Eberhard, 2011) and the araneid *Trichonephila clavipes* (Linnaeus, 1767) (Robinson and Robinson, 1973; Eberhard, 2020), also attack prey rapidly, but many other orb-weaving spiders have relatively shorter legs and are much slower (summary in Eber-

hard, 2020). The typical linyphiid body plan noted above, with relatively long, thin legs, operating in conjunction with their nearly always unobstructed sheets that have an open space below that facilitates rapid movement and robust chelicerae and reduced aciniform spigots associated with rapid biting attacks, suggests specialization for speedy attacks on prey. The linyphiids' legs contrast with the short heavy legs of some slowly attacking orb weavers, such as the araneids *Micrathena* and *Gasteracantha* and theridiosomatids (Eberhard, 2020), and the thick, powerful legs of many webless spiders (Wolff et al., 2022).

One consequence of rapid linyphiid attacks is that the prolonged retention of prey in their webs is probably less crucial for prey capture than it is in orbs: probably only a short retention time (perhaps generally <1 second) is necessary for linyphiids to capture many of their prey. Nielsen (1932) observed that the webs of *Neriene montana* retained flies for only very short periods, and Turnbull (1960) mentions prey that were not attacked readily escaped from webs of this same species. The small droplets of adhesive on linyphiid web lines may be sufficient to achieve momentary retention (Eberhard, 2021). In general, linyphioids may represent an additional example of the pattern noted by Kaston (1964) for web-building species to evolve to rely less on their webs and more on active attack behavior.

We must reemphasize the current lack of data on the presence and distribution of adhesive material in the web, which undoubtedly affect prey retention times. The retention capabilities of the different linyphioid webs probably depend on the presence of sticky lines, the sizes and spacing of the droplets of adhesive, and the densities of sticky (and nonsticky) lines in the sheet and in the upper tangle just above the sheet. Preliminary data from other studies indicate that the fraction of lines in the sheet that bear droplets differs

between species; for example, webs of *Microlinyphia pusilla* had more sticky globules than those of *Linyphia triangularis* (Benjamin et al., 2002). *Nerienne radiata* lacks triads (there are no aggregate gland spigots accompanying the flagelliform spigot) (Schütt, 1995), but the congeneric *N. coosa* had abundant droplets on nearly all of the lines in the sheet (Eberhard, 2021). The numbers of aggregate gland spigots in *Linyphia hortensis* also apparently varied (“in some specimens of *L. hortensis* one of the spigots of the aggregate gland may still exist”; Schütt, 1995: 559). In at least several species of the erigonine genus *Callitrichia* the triad on the posterior lateral spinneret is absent in the adults of both sexes (Lin et al., 2022), but nothing is known of their webs. Further observations of linyphioid lines and the droplets on them under the compound microscope may yield important new insights.

The “elevated sheet with tangles above and below” design that is common in linyphioids has evolved convergently in several other families of spiders, including the theridiids *Nihonhimea tessellata* (Keyserling, 1884), *Cryptachaea* sp., *Tidarren* spp., and *Chrosiothes* sp. (Eberhard et al., 2008; Madrigal-Brenes and Barrantes, 2009); the araneid *Cyrtophora* and allied genera (Blanke, 1972; Eberhard, 2020); and the diguetid *Diguetia* spp. (Eberhard, 1967, 2020; Bentzien, 1973). These webs share the linyphioid trend for a lower tangle less dense than the upper tangle and an open space just below the sheet. Additionally, distant retreats with signal lines that lead to the prey capture webs are widespread in groups with relatively sparse sheets such as the theridiid *Latrodectus*, as well as in many orb weavers (Eberhard, 2020), and are generally lacking in linyphioids. The runways of *Orsonwelles* spp. and the lines that converge at one corner in *Agyreta* spp. that were documented here and that also occur in *Pityohyphantes costatus* (= *Linyphia phrygiana*) (Emerton, 1902) seem to be as

close as linyphiids come to signal lines running to distant retreats; perhaps this lack is related to linyphiid reliance on especially rapid attacks on prey.

Another striking difference between linyphioids and these other families is that linyphioids almost never incorporate objects such as leaves or other detritus into their webs to use them as hiding places (Eberhard et al., 2008; Eberhard, 2020). One web of *Laetesia raveni* apparently had the top of the dome just under leaves (Fig. 33B) that may have provided protection against predators, but the top of the dome was more typical in other webs of the same species (Fig. 32) and of two other *Laetesia* species (GH01 and GH02) (Figs. 33C–F, 34D, E, 35A–E), far from any protecting plant structure. The sheet webs of the African genus *Mecynidis* are typically built under a leaf (Scharff, 1990: fig. 138; Fig. 47A). Webs in one other family, Pholcidae, resembles linyphioids in also building elevated dome-shaped sheets and not using detritus as hiding places. (Their long legs would make hiding this way more difficult.) Pholcids may differ, however, in having only relatively reduced upper tangles, in lacking lower tangles entirely, and in often having larger droplets of adhesive (at least among the few species whose webs are known) (Deeleman-Reinhold, 1986; Eberhard, 1992, 2020; Japyassú and Macagnan, 2004).

Possible Functions

Different portions of linyphiid webs have numerous possible nonexclusive hypothetical functions. For instance, sheets can intercept prey, stop prey, retain prey, protect the spider from prey, transmit vibrations that allow the spider to locate prey, maintain a favorable microclimate for the spider (Toft 1980), and serve as vehicles for pheromones (Nielsen, 1932; Toft, 1980; Schulz and Toft, 1993; Gaskett, 2007). Upper tangles can intercept, stop, and retain prey; provide anchors for lines that tense the

sheet and allow it to curve; and protect the spider from predators. The lower tangles can also protect spiders from predators and provide anchors for tensing the sheet and allowing it to curve. Given that some possible prey appear to sense webs visually and then avoid them (Turnbull, 1960), lower visibility, at least of the sheet and upper tangle, may improve prey capture. Experimental tests of the function of different linyphioid web design details are nearly nonexistent, so we cannot address many of these ideas. Nevertheless, a few aspects of the forms and distributions of web components provide tests of hypotheses regarding functions. Functional considerations can help illuminate significance of the diversity of web forms that we have documented.

Space Below the Sheet for the Spider to Run. This study confirms and extends the observations of Nielsen (1932) that cup-shaped and flat sheets consistently had open spaces just below them. No linyphiid web is known in which there are dense tangle lines immediately below the sheet. As argued by Nielsen, the function of this space is probably to allow the spider to move rapidly under its sheet to attack prey and escape from predators. As far as is known, all linyphioid spiders always move on the undersurfaces of their sheets rather than on top of them, as in *Linyphia triangularis* (Figs. 46A, B), *Neriere albocincta* (Figs. 50C, D), and *Pocobletus* sp. Panama (Figs. 69B, D) (see also Bristowe, 1930; Nielsen, 1932; Suter, 1984; Eberhard, 2022, on *Diplothyron simplicatus*). We have never observed a linyphiid consistently running on the upper surface of a sheet.

In contrast, no similar open spaces were seen between the upper surface of the sheet and the upper tangle. It appeared that the density of the upper tangle tended to be greatest near the upper surface of the sheet and to decrease gradually farther up. Examples include *Frontinella pyramitela* (Figs. 27C, D), *Pocobletus* sp. GH33 (Figs. 68B–D), and *Pocobletus* sp. GH28 (Fig.

70D). Possible exceptions were *Novafrontina uncata* (Fig. 59A), *Neriere digna* (Fig. 50G), *Acroterius* GH02 (Fig. 78), and *Neriere variabilis* (Fig. 53F). Greater tangle density just above the upper surface of the sheet may represent an adaptation for retaining prey that have fallen onto the sheet's surface in the cyrtophorine araneid *Cyrtophora citricola* (Forsskal, 1775), another group that builds a horizontal sheet with an upper tangle that includes many relatively lax lines that may hinder prey movement across the sheet (Eberhard, 2020).

Defense Against Predators. Blackledge et al. (2003) argued that tangle webs have a defensive function. That study, however, focused only on sphecids wasps as predators and was based on the questionable assumption that faunal surveys employing collecting techniques such as beating, sweeping, pitfall trapping, and canopy fogging provide accurate reflections of the relative numbers of prey that are available to these wasps. Additionally, most linyphiids are too small to serve as food for many sphecids wasps (Bristowe, 1941). The study also lumped the many linyphiids that do not build a tangle or a sheet below the main sheet with those that do, so its relevance here is uncertain.

Some data from the present study suggest a defensive function for the lower tangle. That lower tangles were nearly always smaller than the main cup-shaped sheet and were often located just under the bottom of the cup where the spider probably rested in *Laminacauda* sp. (Figs. 43D, E), *Pocobletus* sp. GH32 (Fig. 66C), *Pocobletus* sp. exGH05 (Fig. 72E) supports the hypothesis that the lower tangle has a defensive function. In our experience, spiders with domed or cupped sheets tend to rest under the peak or under the bottom of the cup (further evidence comes from explicit statements to this effect by Emerton (1902) for *Neriere radiata* (= *Linyphia marginata*); by Suter (1984) for *Frontinella pyramitela*; and by Eberhard (2022) for

Diplothyron simplicatus and *Neriere coosa*, as well as from photos of Shinkai (1979) and Shinkai and Takano (1984) for *Turinyphia junohamensis* (Bösenberg & Strand, 1906) and *Neriere emphana* and from our photos of *Neriere albolimbata* (Figs. 50C, D), *Linyphia triangularis* (Figs. 46A, B), and *Pocobletus* sp. Panama (Fig. 69B). The central positions of these lower tangles thus suggest that their most probable function is to form a physical barrier against enemies that attack the spider from below. In addition to being a physical barrier, the lower tangle may also serve as an early warning device to elicit defensive behavior. *Florinda coccinea*, which had a moderately sparse lower tangle that was not concentrated below the center of the sheet, dropped quickly to the substrate below when startled (W. Eberhard, unpublished; G. Hormiga, unpublished), and *Microlinyphia mandibulata* (Emerton, 1882), which apparently lacked a tangle below, also dropped when startled (Emerton, 1902). Behavioral evidence in other families also indicates that a tangle below the spider's resting site (the hub of a horizontal orb) functions to defend uloborid spiders from predators (Lubin et al., 1982; Lubin, 1986; summary in Eberhard, 2020).

Nevertheless, the defensive function hypothesis seems unlikely to explain webs in which the lower tangle consisted of only a few lax lines, some of which were far from the spider's presumed resting site, as in *Pimosa breviata* (Fig. 64E) and *Laetesia raveni* (Fig. 34B). (Unless, as seems unlikely, these species do not suffer significant predation.)

Upper tangles may also at least occasionally function in protection from predators. In accord with this idea, the upper tangle of *Agyneta* sp. CR01 (Fig. 11D) was more or less limited to just above the site where the spider rested near the edge of the sheet. Both the lower and (especially) the upper tangle lines of *Neriere coosa* webs were generally more concentrated just above (as

well as just below) the spider's resting place; peripheral portions of the large sheets of this species often had no tangle lines above them (Eberhard, 2022).

Prey Capture I: Sensing Prey. The webs of *Erigone dentigera* (Emerton, 1902) and (probably) an unidentified Japanese erigonine (Shinkai, 1979) and of the erigonine *Mermessus tridentatus* (Fig. 47F) were attached at many points to the upper tips of moss plants and other objects near the surface of the ground and lacked clear frame lines. This design may represent an adaptation to enable the spider both to sense and to gain rapid access to pedestrian prey like collembolans walking on the substrate at the edge of the web. This interpretation is supported because some erigonines with webs captured pedestrian prey, and adults of *Hypselistes florens* (O. Pickard-Cambridge, 1896) and multiple species of *Erigone* and *Oedothorax* sometimes captured prey in the field without building any web (Wheeler, 1973; Alderweireldt, 1994).

Prey Capture II: Intercepting and Stopping Prey. Tangles above the sheets of linyphioids and other spiders that build sheets, including theridiids, araneids, diguetids, diplurids, agelenids, and lycosids (Eberhard, 2020) are generally considered to be devices for intercepting and stopping prey in the air above the sheet, knocking them down onto the sheet, and then retaining them on the sheet, allowing the spider to attack (Foelix, 2011). For most groups these hypotheses are not supported by empirical studies, but experimental elimination of tangles above the sheet showed that the tangles both increased prey capture and reduced predation in the araneid *Cyrtophora moluccensis* (Dole-schall, 1857) (Blamires et al., 2013). The knock-down hypothesis can explain why upper tangles in our study consistently failed to extend beyond the edges of the sheet, although minor exceptions occurred in *Novafrontina* sp. (Fig. 58A) and *Diplo-*

thyron simplicatus Eberhard (2022). Tangles were nearly as wide as the central sheet, including dome-shaped sheets, as in *Frontinella pyramitela* (Figs. 27C, D); slightly cup-shaped sheets, as in *Pocobletus* sp. exeGH03 (Fig. 72D); and flat or nearly flat sheets, as in *Pocobletus* sp. GH28 (Fig. 71D), *Pocobletus* sp. GH11 (Figs. 70A, B), *Mecynidis* sp. (Figs. 47A–C), and *Tapinopa vara* (Fig. 76B).

In many (although not all) of the webs with substantial upper tangles, the upper tangle diameter decreased the farther above the sheet, and more peripheral portions of the sheet often had fewer knock-down lines above them, as in *Pocobletus* sp. GH28 (Fig. 71B), *Dubiaranea* sp. DE2 (Fig. 23G), *Frontinella pyramitela* (Fig. 27C), and *Neriene helsdingeni* (Fig. 55D). A few exceptions included *Pocobletus* sp. GH33 (Fig. 67C). If prey tend to fall directly downward when they strike the upper tangle (observations are lacking), then the combination of this pattern in the upper tangle and the lower densities of lines near the edges of sheets (Eberhard, 2022) implies that peripheral portions of the web may be less able to stop and retain prey. The functional significance of looser mesh near the web's periphery is not clear and deserves further study.

Prey Capture III: Retaining Prey until the Spider Arrives. The widespread existence of sticky lines in sheets indicates that sheets function in retaining prey. In general, the multiple lines attaching the upper tangle to the sheet produced only tiny or imperceptible dimples in the sheet, implying that these lines were under relatively low tensions compared with those on lines in the sheet. Lax lines just above the sheet, as in *Linyphia triangularis* (Fig. 46E) and *Dubiaranea distincta* (Figs. 21C, D), may be specialized for entangling prey, and thus increasing the time they are retained after falling onto the sheet (similar, apparently especially lax lines just above the sheet occur in the araneid *Cyrtophora citricola*

(Eberhard 2020) and the theridiid *Nihonhimea tessellata* (Jörger and Eberhard, 2006).

Collembola as Prey. There are several indications that collembolans (wingless insects that can hop but not fly, and which thus generally have aerial trajectories that are largely up and down) may be important prey for those linyphioid species that build webs on or very close to the substrate. Bristowe (1941: 292) reported that collembolans were the principal prey of some linyphiids in the UK. In the field, *Bathypantes eumenis*, which builds webs in irregularities in damp rocks, apparently specialized on collembolans (87% of 165 prey in the field belonged to eight species of collembola) (Rybak, 2007), and collembola were the main prey of *Erigone arctica* (White, 1852) (a species with small webs on the substrate; Nielsen, 1932) (Van Wingerden, 1978). Finally, the majority (60%) of the potential prey captured by sticky traps placed in habitats where the webs of at least 11 linyphiid species (including adults and juveniles) were built were collembolans (mostly isotomids and entomobryids, both of which can jump) (Harwood et al., 2001).

In contrast, the linyphiid *Linyphia triangularis*, which builds elevated webs, captured quite different prey. In webs in bushes in a “wet meadow” 90% of the prey from the webs of (apparently adult females) were Aphidoidea, Cicadellidae (= “Cicadina”?) and Nematocera (Nentwig, 1983). In webs in shrubby vegetation of the field layer, 91.6% of 581 prey found in webs of different stages of this species were flying insects, and many were hymenopterans; 7.2% were jumping species (mainly leafhoppers and froghoppers), and only 1.2% were pedestrian (Turnbull, 1960). Weakly flying species (nematocerous flies, parasitic wasps, aphids) were most common, especially early in the season in the webs of juveniles. *Microlinyphia mandibulata* fed largely on leafhoppers (which both jump

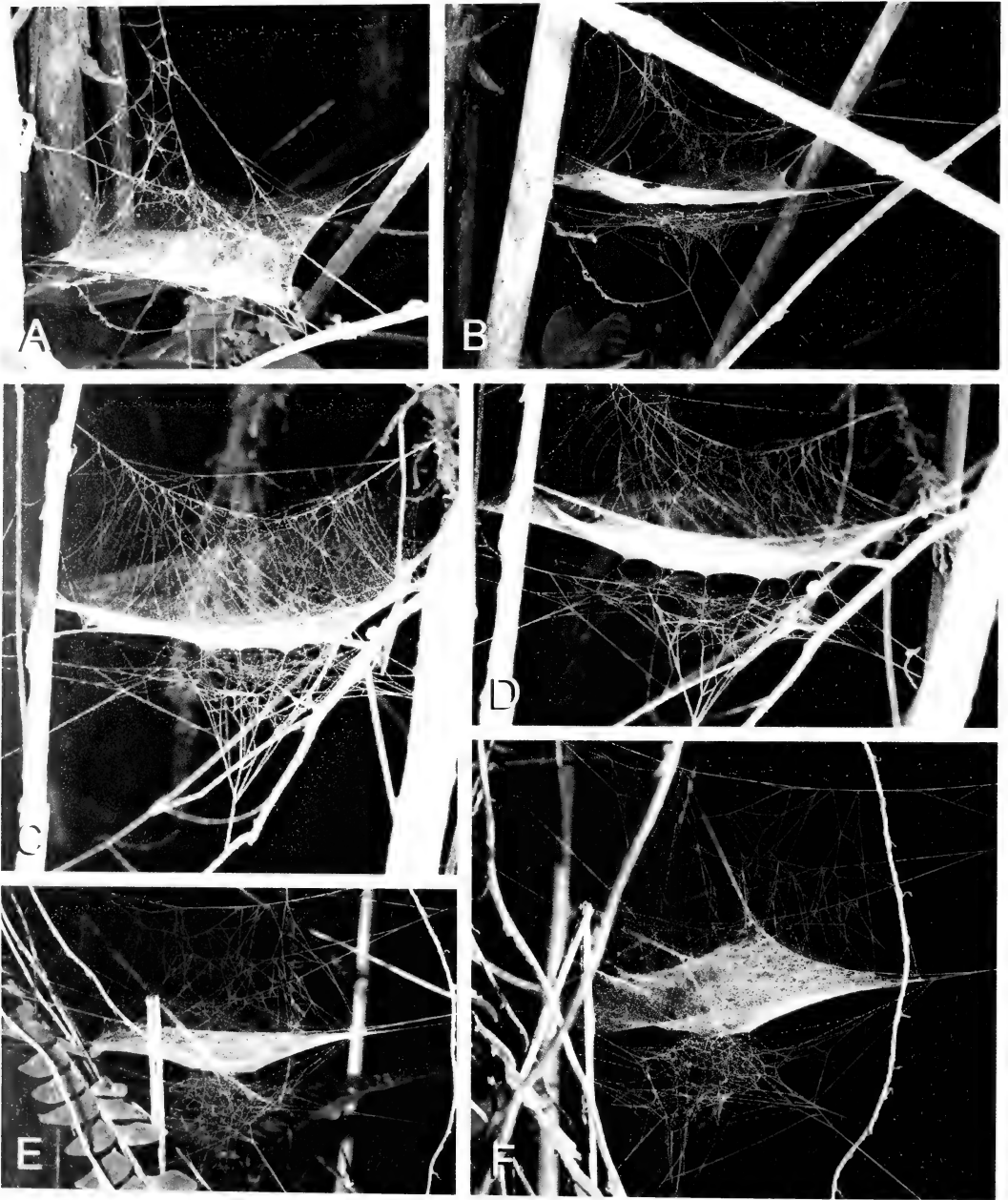


Figure 67. *Pocobletus* webs (2). (A, B) *Pocobletus* sp. GH32, male. Brazil, Rio Jufari (DSC_9294.NEF, DSC_9295.NEF). (C, D) *Pocobletus* sp. GH33, female. Dominican Republic, Sierra de Bahoruco, Reserva Cachote (GH050407_R01_03_DR_Pocobletus_ED.jpg, GH050407_R01_08_DR_Pocobletus_ED.jpg). (E, F) *Pocobletus* sp. GH33, subadult male. Dominican Republic, Sierra de Bahoruco, Reserva Cachote (GH050408_R02_06_DR_Pocobletus_ED.jpg, GH050408_R02_12_DR_Pocobletus_ED.jpg).

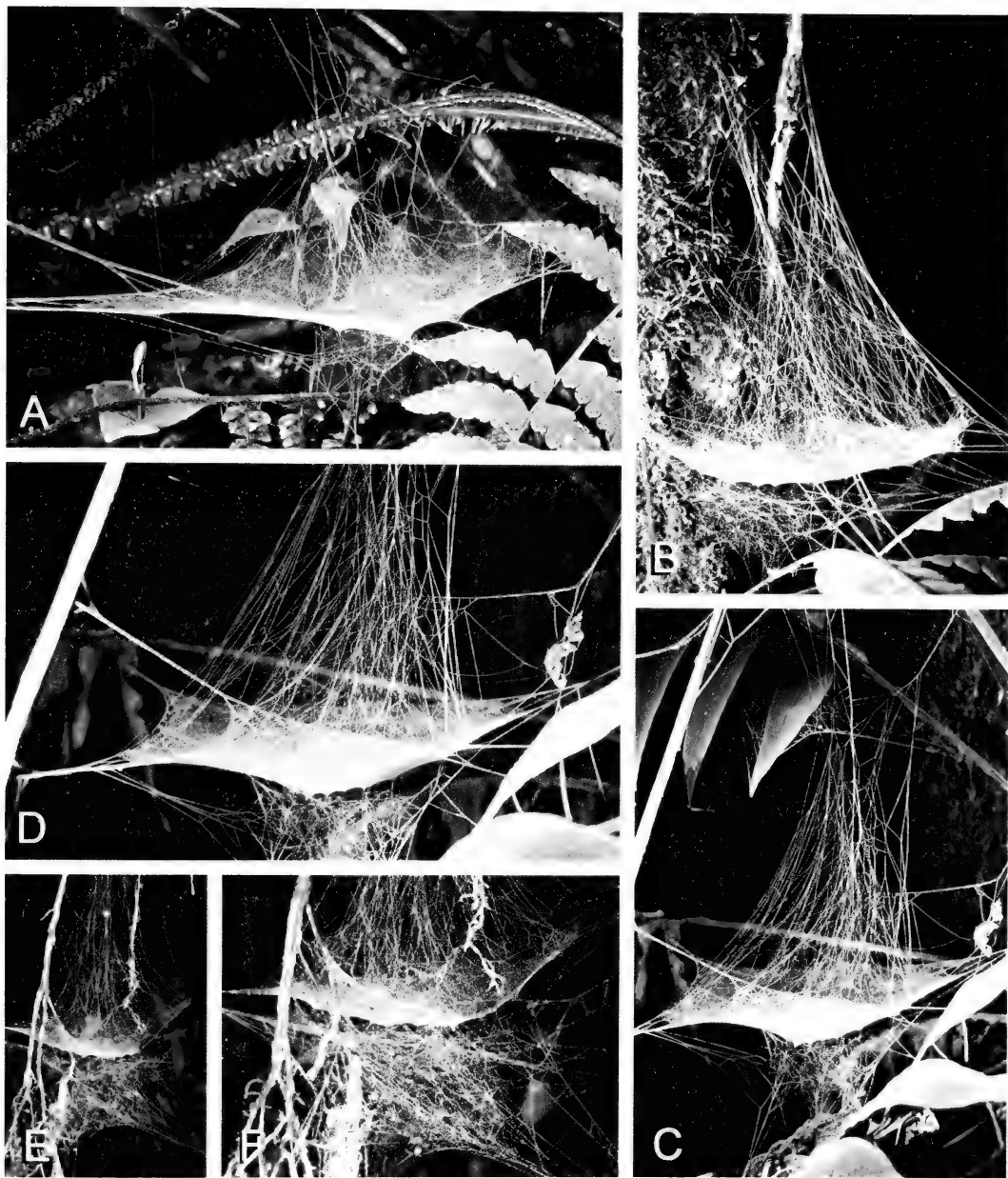


Figure 68. *Pocobletus* webs (3). (A) *Pocobletus* sp. GH33, male. Dominican Republic, Sierra de Bahoruco, Reserva Cachote (GH050408_R01_36_DR_Pocobletus_ED.jpg). (B) *Pocobletus* sp. GH33, female. Dominican Republic, Sierra de Bahoruco, Reserva Cachote (GH050409_R02_36_DR_Pocobletus_ED.jpg). (C, D) *Pocobletus* sp. GH33, female. Dominican Republic, Sierra de Bahoruco, Reserva Cachote (GH050409_R03_01_DR_Pocobletus_ED.jpg, GH050409_R03_07_DR_Pocobletus_ED.jpg). (E, F) *Pocobletus* sp. GH01, female. Panama, Parque Nacional Altos de Campana (DSC_2693_ED.NEF, DSC_2695_ED.NEF).

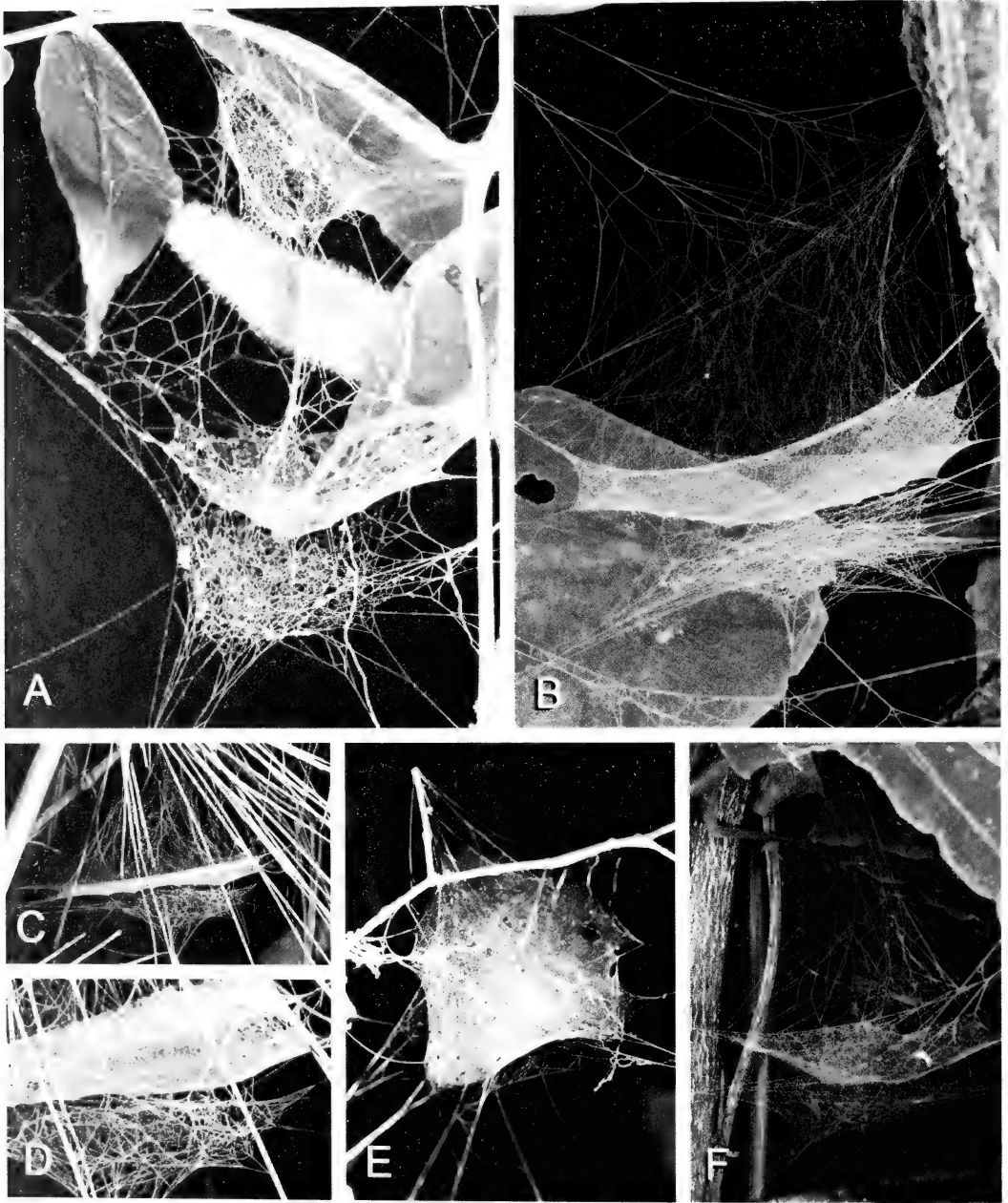


Figure 69. *Pocobletus* webs (4). (A) *Pocobletus* sp. GH01 (female with egg sac, no voucher). Panama, Parque Nacional Altos de Campana (DSC_2866_ED.NEF). (B) *Pocobletus* sp. GH01, female. Panama, Parque Nacional Altos de Campana (DSC_2848_ED.NEF). (C, D) *Pocobletus* sp. GH31, juvenile. Panama, Parque Internacional La Amistad (DSC_4015_ED.NEF, DSC_4023_ED.NEF). (E) *Pocobletus* sp. GH10, female. Ecuador, Parque Nacional Yasuni (GH960621_R07_25_ECU_Pocoblet_sp10_ED.TIF). (F) *Pocobletus* sp. GH01, female. Panama, Parque Nacional Altos de Campana (DSC_2835_ED.NEF).

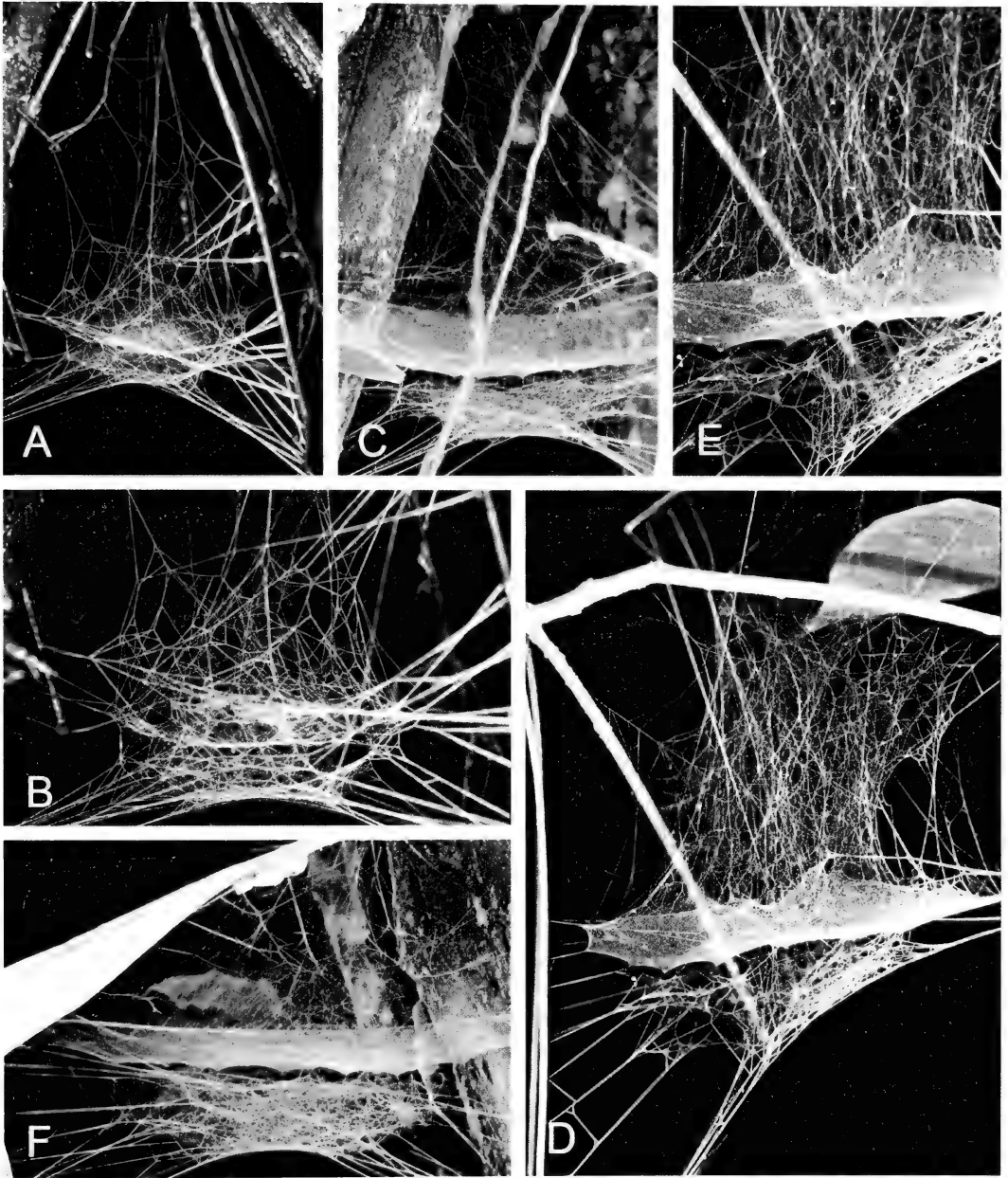


Figure 70. *Pocobletus* webs (5). (A, B) *Pocobletus* sp. GH11, female. Guyana, Gunn's landing strip (GH990716_R07_26_GUY_Pocoblet_sp11_ED.TIF, GH990716_R07_31_GUY_Pocoblet_sp11_ED.TIF). (C) *Pocobletus* sp. GH11, female. Guyana, Gunn's landing strip (GH990706_R03_22_GUY_Pocoblet_sp11_ED.TIF). (D, E) *Pocobletus* sp. GH10, female. Ecuador, Parque Nacional Yasuni (GH960620_R07_13_ECU_Pocoblet_sp10_ED.TIF, GH960620_R07_16_ECU_Pocoblet_sp10_ED.TIF). (F) *Pocobletus* sp. GH11, female. Guyana, Gunn's landing strip (GH990706_R03_20_GUY_Pocoblet_sp11_ED.TIF).

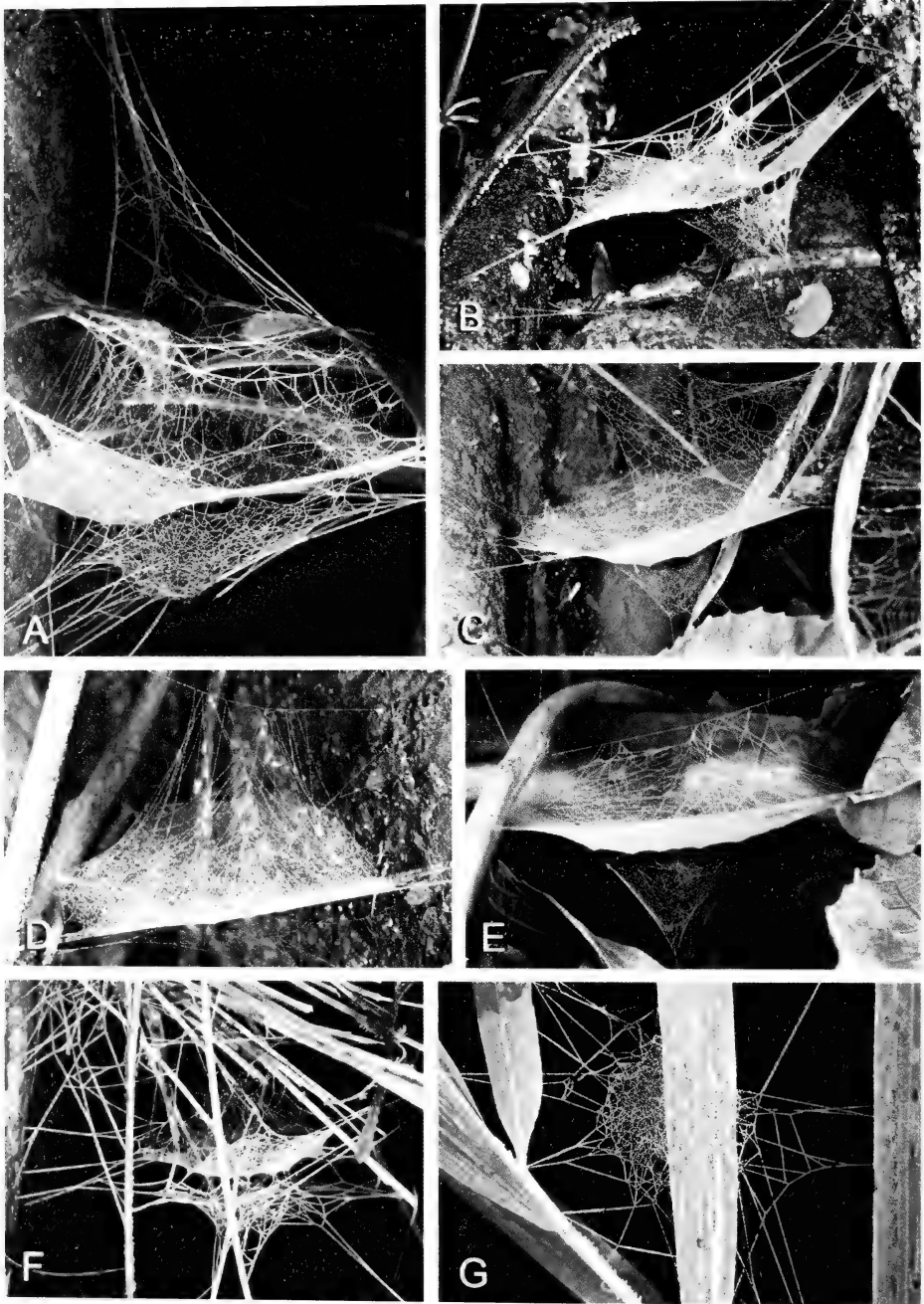


Figure 71. *Pocobletus* webs (6). (A) *Pocobletus* sp. GH11, female. Guyana, Gunn's landing strip (GH990717_R08_03_GUY_Pocoblet_sp11_ED.tif). (B) *Pocobletus* sp. GH28, female. Argentina, Iguazu (MR990713_X01_09_ARG_Pocoblet_sp28_ED.jpg). (C) *Pocobletus* sp. GH28, female. Argentina, Iguazu (MR990716_X00_01_ARG_Pocoblet_sp28_ED.jpg). (D) *Pocobletus* sp. GH28, sex? Argentina, Iguazu (MR990716_X00_03_ARG_Pocoblet_sp28_ED.jpg). (E) *Pocobletus* sp. GH28, female. Argentina, Iguazu (MR990716_X16_36_ARG_Pocoblet_sp28_ED.jpg). (F) *Pocobletus* sp. GH03 subadult female. Ecuador, Napo, Sierra Azul (GH960614_R00_25_ECU_Pocoblet_sp3_ED.tif). (G) *Pocobletus* sp. GH03, male. Ecuador, Napo, Sierra Azul (GH960614_R02_18_ECU_Pocoblet_sp3_ED.tif) (photos B–E by Martin J. Ramirez).

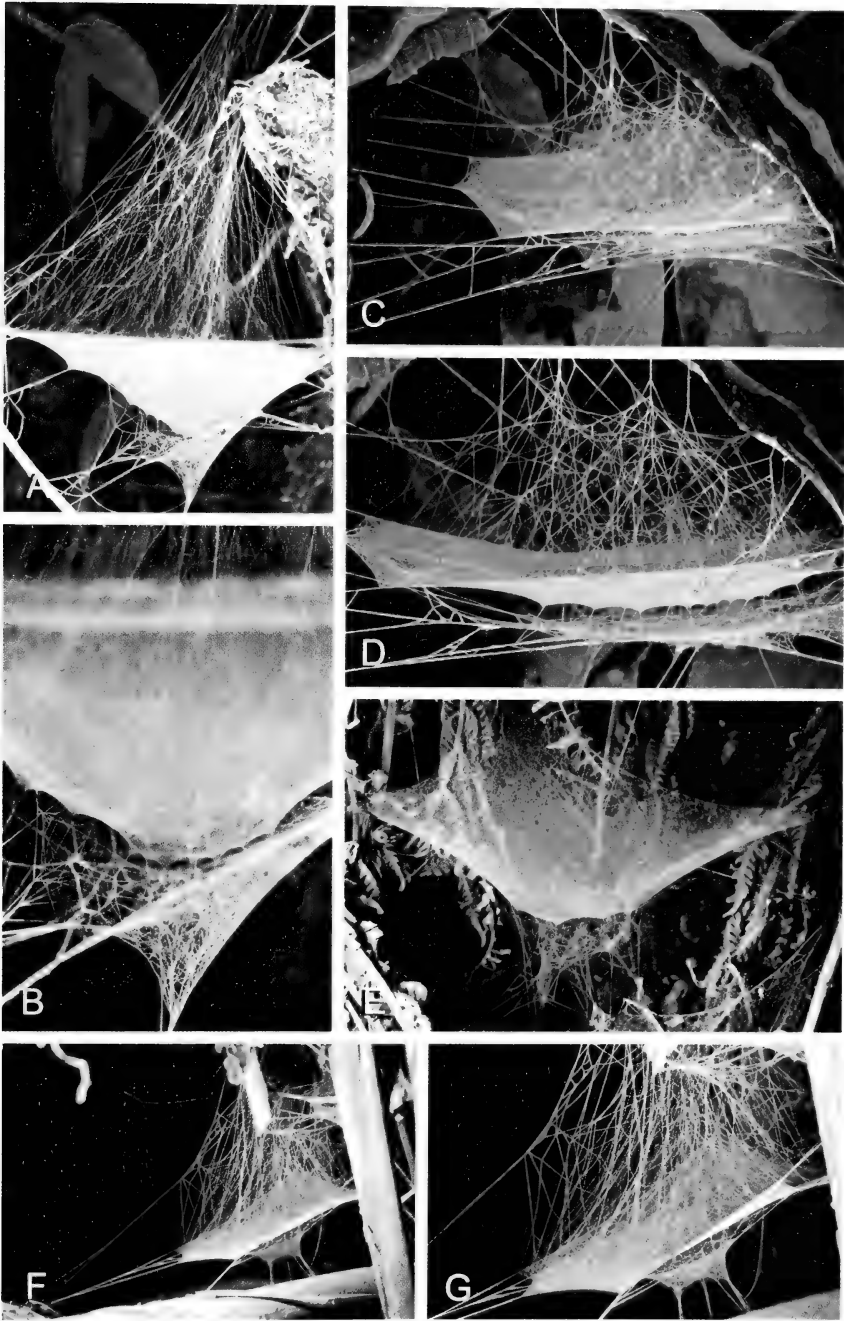


Figure 72. *Pocobletus* webs (7). (A, B) *Pocobletus* sp. GH03, female. Ecuador, Napo, Sierra Azul (GH960612_R01_27_ECU_Pocoblet_sp3ED.tif, GH960612_R01_32_ECU_Pocoblet_sp3ED.tif). (C, D) *Pocobletus* sp. exeGH03, female. Colombia, near Cali (GH980211_R00_19_COL_Exechop_sp3_ED.tif, GH980211_R00_21_COL_Exechop_sp3_ED.tif). (E) *Pocobletus* sp. exeGH05, female. Colombia, Cundinamarca (GH980201_R00_09_COL_Exechop_sp5_ED.tif). (F, G) *Pocobletus versicolor* (Millidge, 1991), juvenile. Costa Rica, Estación Biológica La Selva (GH930403_R06_01_CRI_Exechop_versic_ED.tif, GH930403_R06_07_CRI_Exechop_versic_ED.tif).

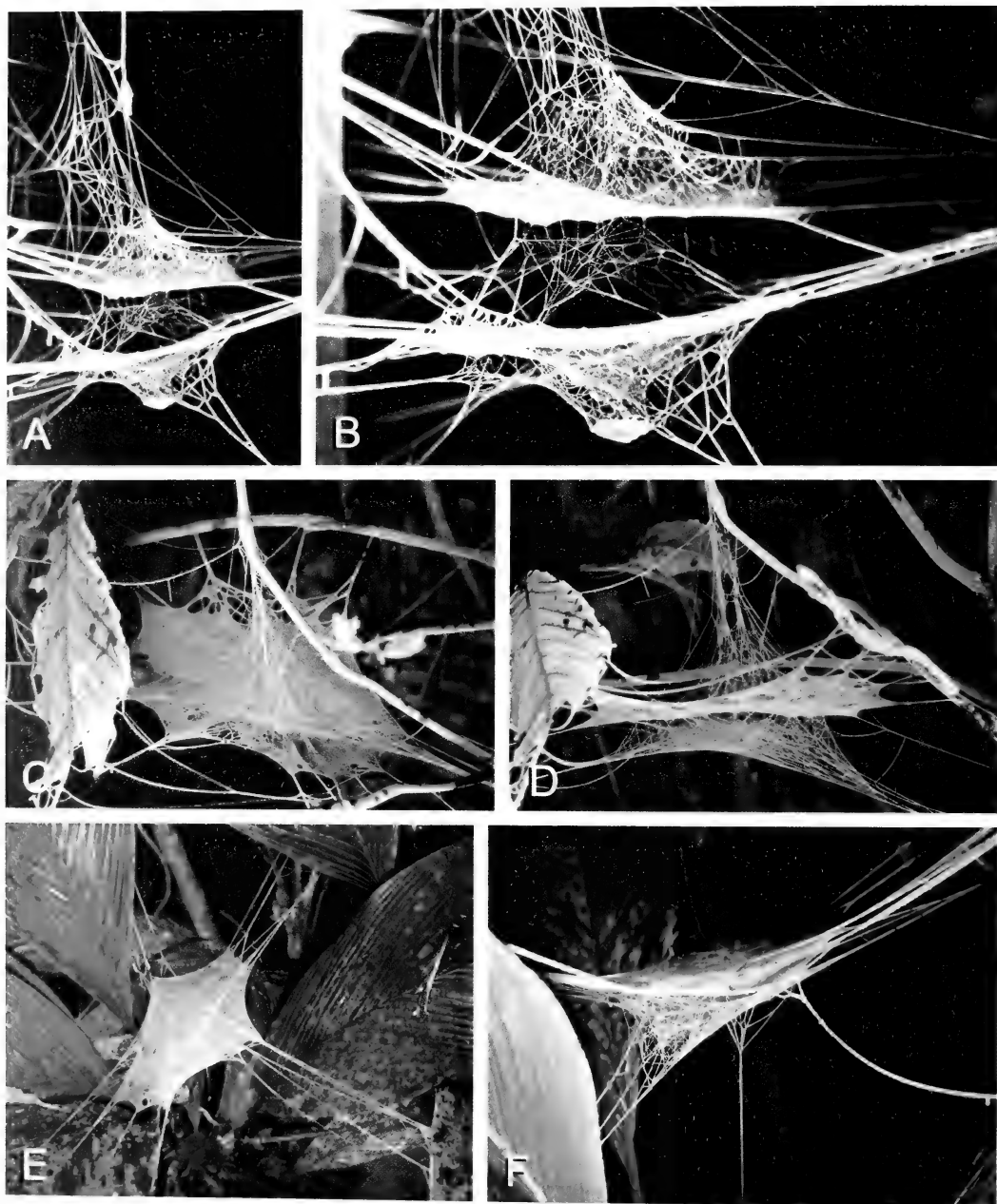


Figure 73. *Pocobletus* webs (8). (A, B) *Pocobletus versicolor* (Millidge, 1991), male. Ecuador, Parque Nacional Yasuni (GH960621_R07_20_ECU_Exechop_versic_ED.TIF, GH960621_R07_21_ECU_Exechop_versic_ED.TIF). (C, D) *Pocobletus versicolor* (Millidge, 1991), female. Costa Rica. Estación Biológica La Selva (GH930405_R08_11_CRI_Exechop_versic_ED.TIF, GH930405_R08_14_CRI_Exechop_versic_ED.TIF). (E, F) *Pocobletus versicolor* (Millidge, 1991), female (E, sheet web seen from above; F, lateral view of the same web) Costa Rica. Estación Biológica La Selva (GH930405_R08_25_CRI_Exechop_versic_ED.TIF, GH930405_R08_21_CRI_Exechop_versic_ED.TIF).

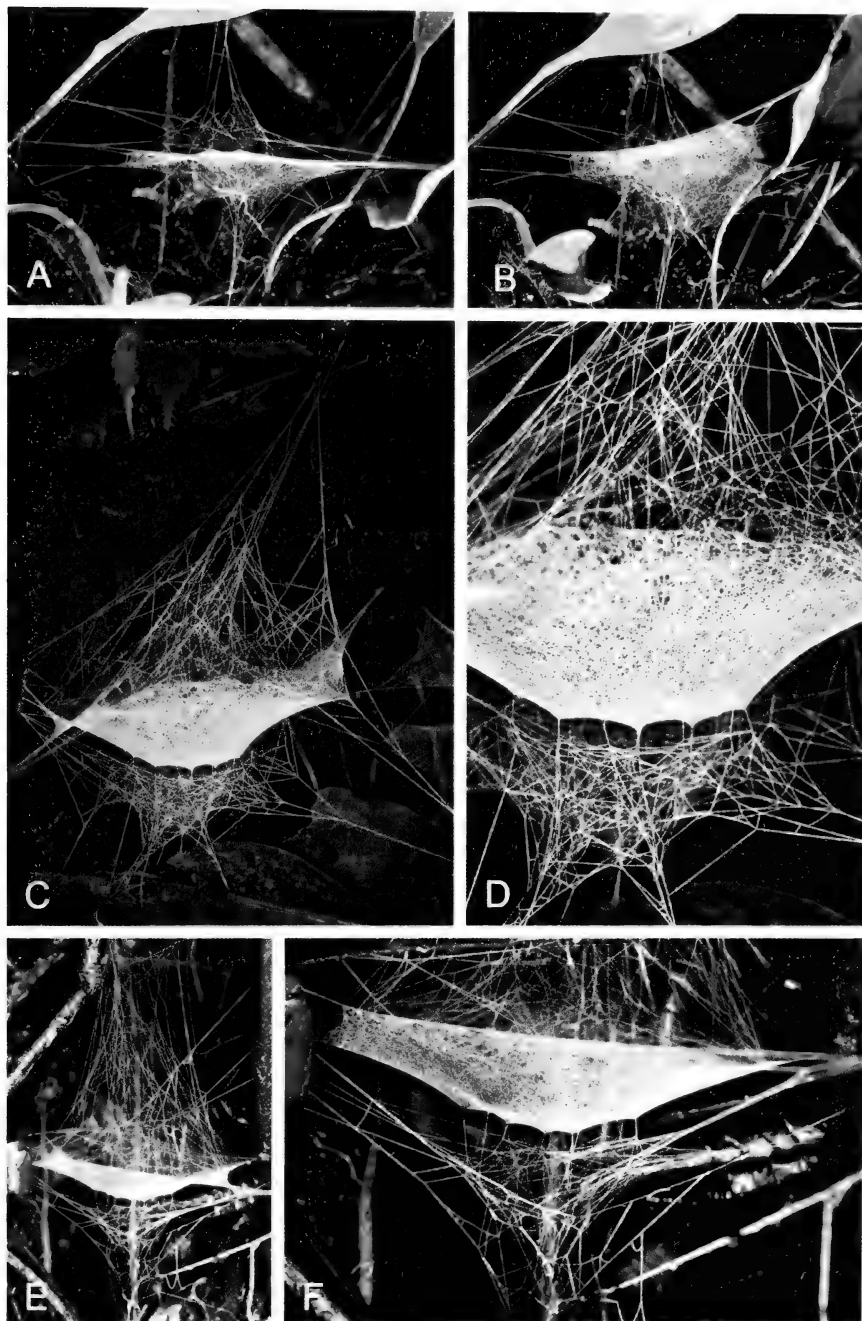


Figure 74. *Pocobletus* webs (9). (A, B) *Pocobletus* sp. exoGH01, juvenile. Costa Rica, Cerro Pittier, Parque Internacional La Amistad (GH950612_R00_14_CRI_Exocora_sp1_ED.tif, GH950612_R00_15_CRI_Exocora_sp1_ED.tif). (C, D) *Pocobletus* sp. exoGH02, female. Costa Rica, Cerro Pittier, Parque Internacional La Amistad (GH950612_R00_17_CRI_Exocora_sp2_ED.tif, GH950612_R00_22_CRI_Exocora_sp2_ED.tif). (E, F) *Pocobletus* sp. exoGH02, female. Costa Rica, Cerro Pittier, Parque Internacional La Amistad (GH950613_R00_30_CRI_Exocora_sp2_ED.tif, GH950613_R00_32_CRI_Exocora_sp2_ED.tif).

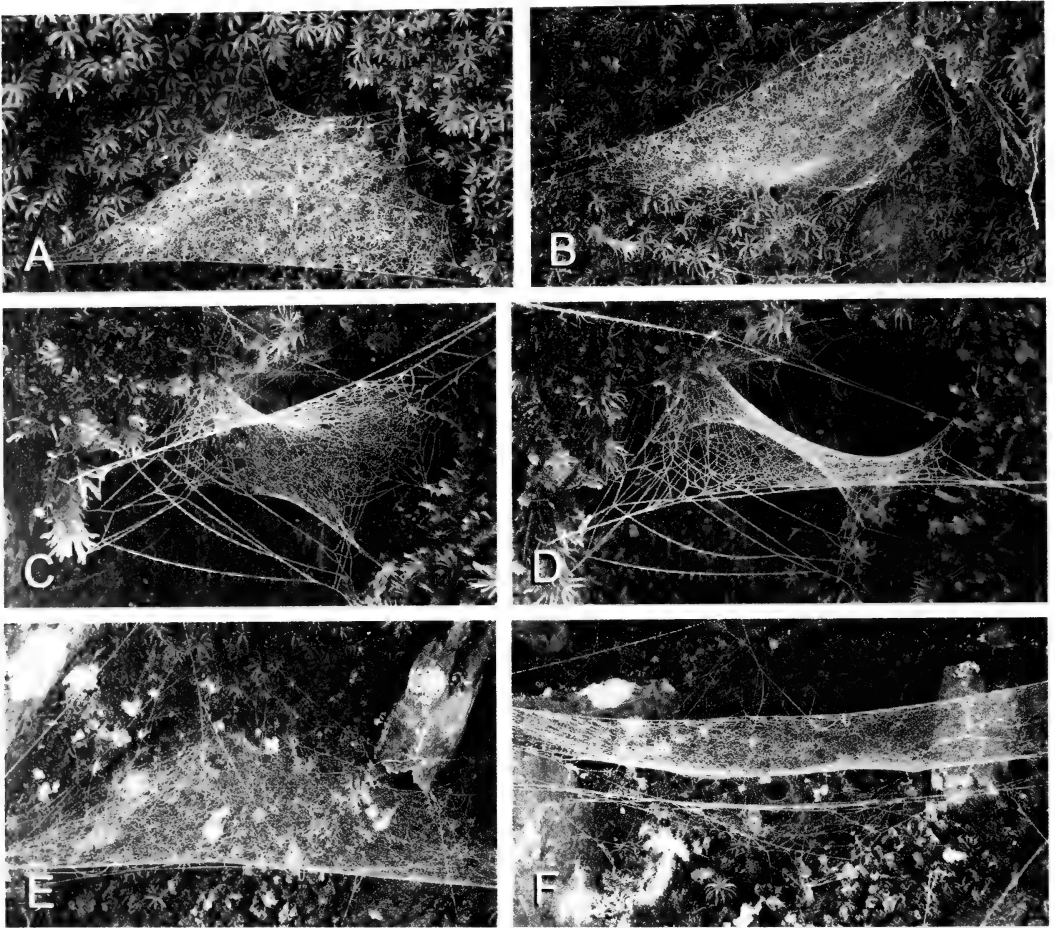


Figure 75. *Putaoa seediq* webs. (A, B) *Putaoa seediq* Hormiga & Dimitrov, 2017, subadult female. Taiwan, Huisun Forestry Station, Xiaochu Mtn. (A) Sheet web, from above. (B) Same web as in A, from below, showing retreat entrance funnel (DSC_1012_ED.NEF, DSC_1014_ED.NEF). (C, D) *Putaoa seediq*, juvenile. Taiwan, Huisun Forestry Station, Xiaochu Mtn. Lampshade web, slightly from below. (D) Same as in C, from the side (DSC_1030_ED.NEF, DSC_1031_ED.NEF). (E, F) *Putaoa seediq*, juvenile. Taiwan, Huisun Forestry Station, Xiaochu Mtn. Sheet web, from above. (F) Same web as in E, from below, showing retreat entrance funnel (DSC_1022_ED.NEF, DSC_1025_ED.NEF).

and fly) and small dipterans in alfalfa fields (Wheeler, 1973), while both *Bathypantes gracilis* and *Neriere clathrata* in cultivated fields fed mostly (91% and 66%, respectively) on aphids and collembolans (Alderweireldt, 1994).

Water Droplets as Traps? Some sheet-building species, such as *Agyneta* sp. CR01 (Fig. 11E), *Agyneta* sp. (Fig. 13A), and *Tapinopa longidens* (Fig. 76A), consistently build webs extremely close to damp sub-

strates such as wet moss or earth. The cooler air at such a site holds less water than warm air, and water condenses from oversaturated air on anything that can provide a nucleus and then breaks into droplets because of Raleigh instability. Spider webs, such as those of some erigonines that are built in the very humid layer close to a damp substrate, are often covered with tiny water droplets, as in *Erigone dentigera* (Emerton, 1902) and *E.*

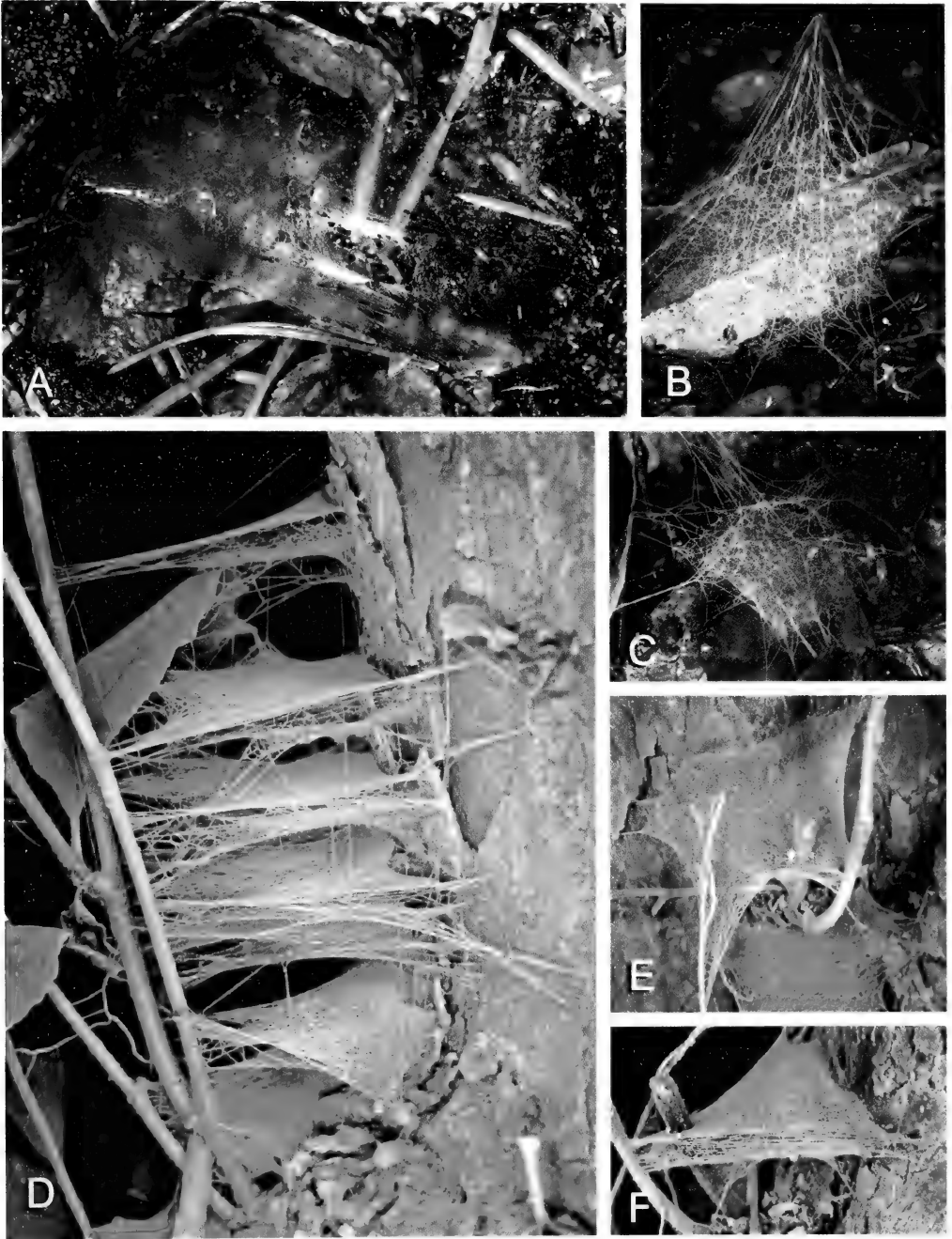


Figure 76. *Tapinopa* webs. (A) *Tapinopa longidens* (Wider, 1834), female (spider is at the top center of image). Sweden, Tullbotorp (GH940815_R00_14_SWE_Tapin_longi.tif). (B, C) *Tapinopa vara* Locket, 1982, female. Thailand, Naratiwat, Hala Bala (GH031013_R06_05_THA_ED.TIF, GH031013_R06_03_THA_ED.TIF). (D) *Tapinopa bilineata* Banks, 1893, juvenile. USA, Maryland, Patuxent Wildlife Research Center (GH940621_R00_27_USA_Tapinopa_ED.TIF). (E, F) *Tapinopa bilineata* Banks, 1893, juvenile. USA, Maryland, Patuxent Wildlife Research Center (GH940621_R00_23_USA_Tapinopa_ED, GH940621_R00_24_USA_Tapinopa_ED).

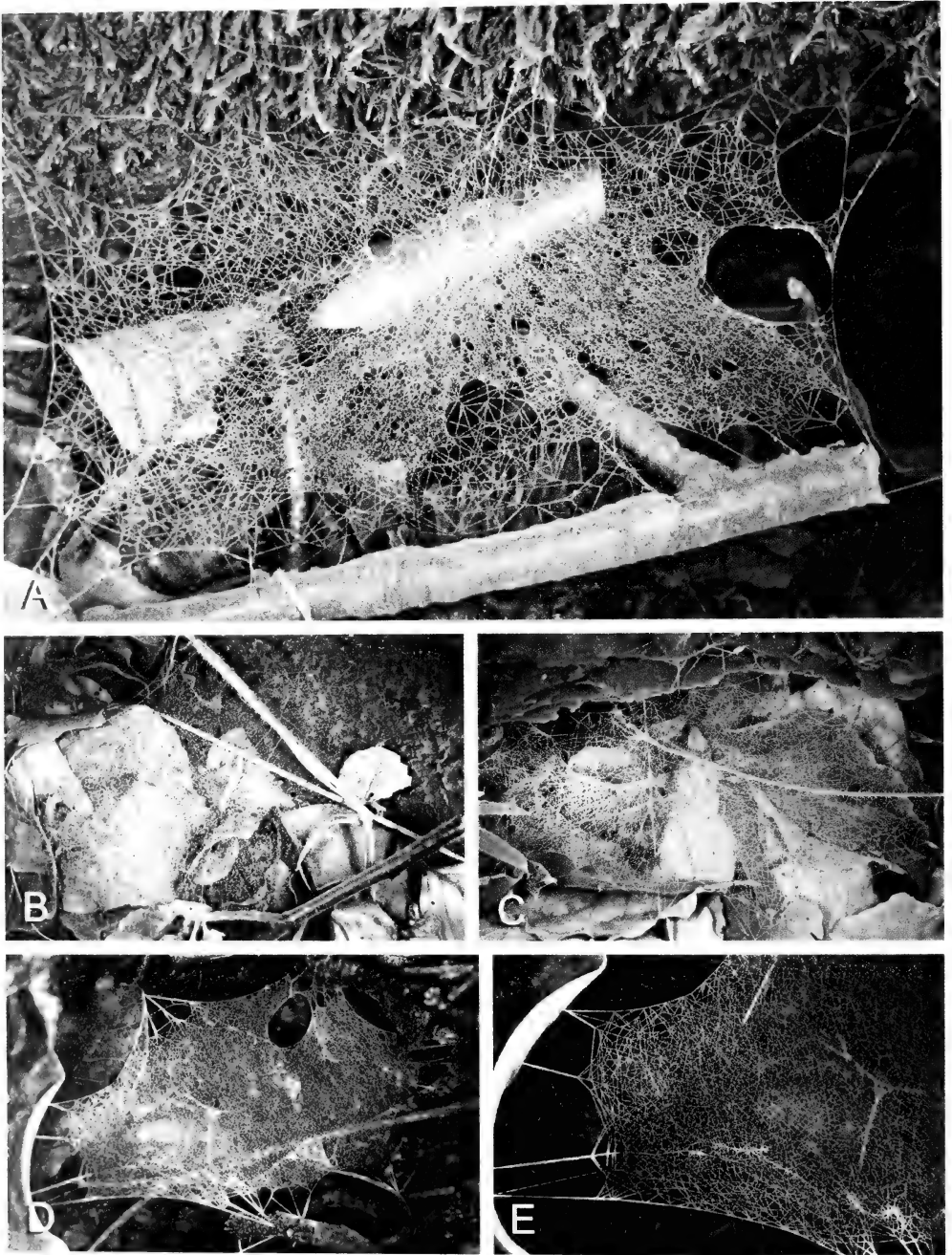


Figure 77 *Tenuiphantes* and *Walckenaeria?* webs. (A) *Tenuiphantes flavipes* (Blackwall, 1854), female. Denmark, Hestehaven (GH940901_R00_11_DEN_Tenuiph_flav_ED.TIF). (B) *Tenuiphantes flavipes*, female. Denmark, Hestehaven (GH940901_R00_33_DEN_Tenuiph_flav_ED.TIF). (C) *Tenuiphantes flavipes*, female. Denmark, Hestehaven (GH940901_R00_12_DEN_Tenuiph_flav_ED.TIF). (D, E) *Walckenaeria?* sp., female. Costa Rica, Parque Internacional La Amistad Cerro Pittier (GH950613_R00_36_CRI_Walcken_ED.TIF, GH950613_R00_37_CRI_Walcken_ED.TIF).



Figure 78. *Acroterius* webs (1). *Acroterius* GH02, subadult male. Taiwan, forest north of Dungyuan (DSC_0964.NEF).

atra (Nielsen, 1932). Such droplets may function in prey capture in the webs of a hahniid spider: prey that struggled to free themselves on droplet-covered sheets sometimes accumulated a larger drop of water on their bodies that appeared to impede their escape (Eberhard, 2019). It remains to be determined whether by building in such habitats linyphiids provide their webs with water droplets that facilitate prey capture.

Forms of the Sheet—Cups, Domes, Dimples, etc. The functional significance of the domed, cup-shaped, and flat forms of sheets is unclear. One might suppose that the upward-slanting curves of cup-shaped sheets function to make it more difficult for prey to walk off the sheet, but this idea runs counter to the more widespread trend

toward domed sheets, a design that would by this reasoning *promote* prey escape. Domed sheets are widespread in pholcids, and also occur in some theridiids (Madrigal-Brenes and Barrantes, 2009; Eberhard, 2020). Domed sheets were always accompanied by a tangle above the sheet, and cup-shaped sheets by a tangle below, but these correlations are probably because of construction constraints: the lines in a sheet are not stiff, so additional lines out of the plane of the sheet are needed to hold the sheet in a curved configuration. Nevertheless, the relatively small tangles associated with strongly domed pholcid sheets show that relatively small tangles can be sufficient to sustain sharply domed sheets (see Eberhard, 2020, on *Modisimus*). The runways from apparent resting places near the substrate to the sheet, as in *Himalaphantes* sp. (Figs. 28B, D, E), presumably function to allow the spider to rest in a less exposed position and reduce the danger from predators but nevertheless allow rapid access to the sheet for prey capture.

The sites of dimples in sheets suggest their possible functions. Dimples tended to occur at places where the sheet was curved, with the dimple projecting in the opposite direction from the sheet's curve. For instance, relatively uniformly spaced downward dimples occurred in the uniformly curved cup of one web of *Acroterius* sp. GH02 (Fig. 78) but were more concentrated near the centers of other, less sharply cup-shaped sheets of the same species (Figs. 79D, F). The downward-directed dimples in the weakly cup-shaped sheet of *Pocobletus* sp. GH33, in which the curve was mostly limited to the central area, were also limited to the central portion of the sheet (Figs. 67C–F). The dimples were dispersed over nearly the entire sheet in the more uniform, moderately curved cup-shaped sheets of *Frontinella pyramitela* (Figs. 27C, D) (as also reported by Suter, 1984) and of *Frontinella* sp. (Figs. 27A, B). Similarly, upward dimples occurred near

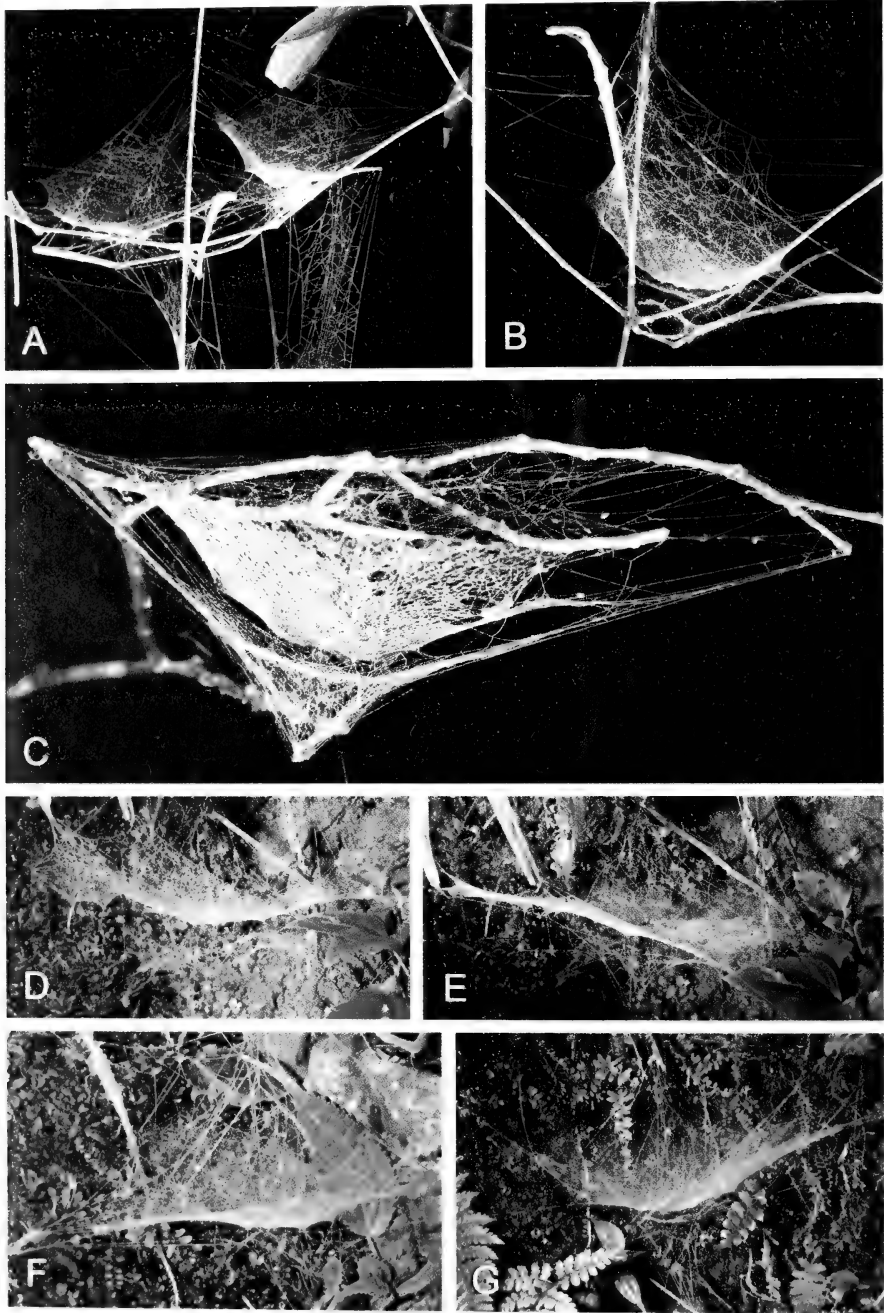


Figure 79. *Acroterius* webs (2). (A) *Acroterius* GH02, juvenile. Taiwan, forest north of Dungyuan (DSC_0975.NEF). (B) *Acroterius* GH02, juvenile. Taiwan, forest north of Dungyuan (DSC_0959.NEF). (C) *Acroterius* GH02, female. Taiwan, Forest N of Dungyuan (DSC_0938.NEF). (D, E) *Acroterius* GH01, male. Thailand, Chiang Mai, Doi Inthanon (GH031004_R03_21_THA_ED.TIF, GH031004_R03_22_THA_ED.TIF). (F) *Acroterius* GH01, subadult female. Thailand, Chiang Mai, Doi Inthanon (GH031004_R03_25_THA_ED.TIF). (G) *Acroterius* GH01, subadult female. Thailand, Chiang Mai, Doi Inthanon (GH031004_R03_29_THA_ED.TIF).

the tops of domes. The small upward dimples in *Diplothyron diana*e (Fig. 20D) and *Grammonota* sp. (Fig. 28A) were at places where an otherwise flat or slightly domed sheet curved downward.

Similar downward-directed dimples occurred where sombrero-shaped sheets curved upward in several other families, including Diguettidae, Araneidae, and Theridiidae (Eberhard et al., 2008; Eberhard, 2020).

The “tensor” lines perpendicular to the sheet that are associated with dimples probably alter the form of the sheet by pulling it downward. In accord with this idea, cutting some tensor lines in *Frontinella pyramitela* webs caused sheets to become flatter (Suter 1984). These lines may also function to tense the sheet itself (Suter 1984). This duality of function is suggested by the weak dimples in the strongly curved (but perhaps not strongly tensed) sheet of Australian genus 3 GH02 (Fig. 18F). Whatever their function, it seems likely that the tensor lines below cup-shaped sheets must constitute physical obstacles that reduce the speed with which spiders can attack prey; their function must be important enough to compensate for this hinderance to the spider’s attacks. It appears, in contrast, that the striking absence of strong upward-directed dimples with tensor lines in dome-shaped sheets, even sharply dome-shaped sheets such as *Neriene litigiosa* (Fig. 56), is associated with many different lines that attach the sheet to the tangle at different sites, instead of just a few tensor lines. This difference may be associated with lack of selection on lines just above the sheet to facilitate rapid attacks.

Mechanical Stability. Peters and Kooor (1991) stated that the only function of tangles is to support the sheet. The numerous sheet webs that lacked or nearly lacked upper or lower tangles argue against this idea. Nevertheless, a sheet obviously needs some lines to provide mechanical support, especially to resist stresses such as

wind and falling detritus. This function cannot be examined for lack of data. An incidental observation was that many linyphiid webs often survive rain storms more or less intact. The sheets of some *Diplothyron simplicatus* webs, which have extensive tangles above and below, had repaired sectors of the sheet (Eberhard, 2022). Even species with naked or nearly naked sheets sometimes had repairs of damage to their sheets, as in *Floronina bucculenta* (Figs. 26D, E) and *Tenuiphantes flavipes* (Figs. 77A–C), suggesting that these webs may have relatively long functional lives in nature.

The Mystery of Naked Sheets. The frequent absence of upper tangles in some linyphioids (11 species in perhaps 10 different genera had “naked” or “nearly naked” sheets), and the sparse lines above the sheets of others such as the undescribed species Australian genus 3 (Fig. 18E) (which nevertheless had an extensive tangle below), as well as the naked sheets typical of Cyatholipidae (Figs. 3–7), constitutes a puzzle: it is not clear how prey are captured by horizontal sheet webs that lack tangles. One unavoidable conclusion seems to be that many prey in the field must be moving through the air in vertical rather than horizontal directions. Perhaps, for example, the sheets of webs that are located just above but very close to the substrate (and in which tangles were usually reduced or absent) function to capture jumping collembolans.

It is striking that almost all the webs in this study that were found near the ground lacked a tall or thick upper tangle (the exception is one web of *Novafrontina uncata* on the forest floor; Figs. 58C, D). The existence of a few, sparse lines above many of these nearly naked sheets showed that attachment points were nevertheless available, eliminating the possibility that the spiders could not build lines above their sheets. The implication is that these webs were capturing prey that were moving

vertically in the air very near the ground. Hahniids also build approximately horizontal sheets very near the ground without tangles above them (Opell and Beatty, 1976; Eberhard, 2019).

This trend in linyphiid webs near the substrate emphasizes the even more general mystery of how prey are captured by the many sheet webs that lack upper tangles, both those built near the substrate and far above it. The low numbers of attachments of these sheets to the substrate suggest that they capture few pedestrian prey; they would seem to be limited to capturing jumping or falling prey (see also Harwood et al., 2001). At least for naked and nearly naked sheets near the ground, perhaps collembolans are the major prey (above). Another possibility, mentioned in connection with symphytognathoid webs near the ground, that they are designed to capture spores or pollen (Blackledge et al., 2011), is contradicted by the lack of any tendency in the spiders in any of these groups to build their sheets just below fungal fruiting structures, as occurs in the specialized spore-feeding mycetophilid fly larvae (Eberhard, 1970).

The small, flat, horizontal, naked sheets of “juvenile” webs of *Bathypantes eumenis* are built in irregularities in damp rocks. Juvenile webs accounted for most prey captures that occurred in captivity (Rybak, 2007), and in the field this species is apparently a specialist on collembolans (87% of 165 prey in the field belonged to eight species of collembola; the different web types were not distinguished in the field) (Rybak, 2007). It appears that these webs have low numbers of attachments to the substrate (only drawings are available), so the alternative possibility that these webs function as sensors for pedestrian prey, as proposed above for erigonine webs, is unlikely.

Capture of collembolan prey does not explain, however, elevated sheets that also lack tangles above them, such as Australian

genus 3 GH02 (Fig. 18E). Similar designs also occur in other spider families, including cyatholipids (Figs. 3–7), oxyopids (Coville and Coville, 1980; Griswold, 1983), psechrids (Robinson and Lubin, 1979; Eberhard, 1987), and synotaxids (Eberhard, 2020). The upper tangles of many pholcids are also very low and seem poorly designed for intercepting prey; some (e.g., *Modisimus bibrri*) are built near the undersides of leaves (Eberhard, 2020). Studies of prey captured in the field could help solve some of these mysteries.

In a striking contrast, the symphytognathoid orb weaver families Anapidae and Symphytognathidae that build orbs in leaf litter close to the ground have evolved to do just the opposite—to add a tangle with both sticky and nonsticky lines above their horizontal webs (Lopardo et al., 2011; Eberhard, 2020).

Summary. The various probable functions of different design details of linyphioid webs described above offer a starting point for understanding the significance of the diversity of web forms documented in this study. Different web designs presumably represent specializations to improve particular functional traits. Although there have been almost no experimental studies of function or of how prey capture occurs that have enough detail to begin to reveal the functions of different design features of linyphiid webs, our overview of web diversity is sufficient to begin a tentative discussion of rapid runs to attack prey, defense against predators, prey interception, prey retention times, collembola in webs near the ground, dimples in sheets and their associated tensor lines, and mechanical stability. Many mysteries remain. Perhaps the greatest is the functional significance of building sheets that are either domed, cup-shaped, or flat—a mystery not only in linyphioids, but also in other groups that build aerial sheets, such as pholcids, theridiids, araneids, and diguetids (Eberhard, 2020).

The Linyphioid Syndrome

As noted in the Introduction, linyphioids comprise a large number of species but are relatively uniform rather than diverse in many somatic morphological traits. This study, in combination with previous publications, has documented a similar pattern of relative uniformity in building a horizontal, unobstructed sheet of some kind, with an open space just under the sheet. We have also documented a substantial amount of diversity in the details of this basic web design that includes the sizes, densities, and locations of tangles above and below the sheet; cupped compared with domed compared with flat sheets; sheets with and without dimples; and sheets with and without retreats at one edge. In general, the appropriate phrase for linyphioid webs is “moderate diversity.” Thus, the linyphiid success story of many species that are often very abundant is perhaps characterized not by evolutionary inventiveness, but by relative conservatism in a suite of traits.

We propose that a subset of this suite of conserved linyphiid traits, including the designs of their webs and the spiders’ morphology and attack behavior, all contribute to increasing the speed with which linyphiids attack their prey. Linyphioid webs appear to have limited retention capabilities, with lines that bear only tiny droplets of adhesive. (The droplets may self-assemble at or near the point of impact and increase adhesion to prey, at least slightly [Eberhard, 2021].) This limited retention capability in webs is combined with very rapid attacks on prey. The horizontal sheet provides a direct path to prey on any portion of the sheet; the smooth surface of the sheet, the almost universal lack of any objects projecting through it, and the open space just below it except the reduced numbers of lines that connect the sheet to the tangle below where the sheet curves upward, all facilitate rapid dashes. The typical spider somatic morphology, in

particular the moderately long, moderately thin legs (in contrast, e.g., with many “stubby-legged” body designs in related groups such as orb-weaving araneoids), also facilitate rapid running. Also contributing to the rapid attacks are immediate biting attacks on prey (rather than wrapping it) used by linyphiids to restrain the prey as soon as the spider arrives (Eberhard, 1967). Biting and then holding on to the struggling prey is facilitated by the robust chelicerae, and perhaps also by the teeth on both margins of the paturon (the basal cheliceral segment) (Draney and Buckle, 2017). Additionally, these biting attacks may explain the reduction in the aciniform gland spigots that provide wrapping silk; the widespread nature of this reduction in linyphiids implies that biting attacks occur in many species whose behavior has yet to be observed. Other web traits also contribute to rapid attacks: the sheet is thin, with most or all lines in nearly the same plane, so the spider can bite the prey through the sheet and grasp it without having to pause to make a hole. Additionally, the sheet is between the spider and the prey and thus protects the spider from damage from the prey’s struggles when the spider contacts the prey while biting and holding it. Still another aspect of typical linyphiid behavior that may also facilitate rapid attacks occurs before the arrival of prey: the spider commonly positions itself near the center of the sheet (Bristowe, 1941; Benjamin and Zschokke, 2002) (although with exceptions that hide in retreats off the center during the day: apparently, early diverging linyphioids; and at least some species in *Pimoida*, *Putoida*, *Stemonyphantes*, and *Labulla*), thus minimizing the distance that it needs to run to reach prey on the sheet, increasing attack speed. This “fast-attack” strategy is also feasible without a web, and may have thus predisposed some members of the large subfamily Erigoninae to lose webs, although the full extent of the absence of foraging webs in erigonines is unknown.

This suite of linyphiid traits (“the linyphiid syndrome”) contrasts with spiders that have thick or only moderately long legs, like theraphosids, ctenids, and lycosids. These species are built to be able to overcome prey by raw physical force, with their legs forcefully pressing the struggling prey against the spider’s chelicerae (e.g., Rovner, 1978, 1980). Some other groups, like theridiosomatids and *Hyptiotes* (Uloboridae), also have relatively thick legs, to develop the force necessary to tense their webs (ditto the araneids *Gasteracantha* and *Micrathena*, which do not run rapidly to the prey when it strikes the web, but rather jerk the web). At the other end of the spectrum are spiders like pholcids with thin and very long legs that also run very rapidly but bite only briefly an extremity of their prey and rely on silk (wrapping + web) to immobilize prey (Eberhard, 2020). Relatively long legs are also associated with rapid running in the salticid *Megaloastia mainae* Žabka, 1995 (Soley et al., 2016). The linyphiid syndrome is near the pholcid end of this spectrum.

These tentative correlations between behavior and morphology seem to contrast sharply with the findings by Wolff et al. (2022: 1) that few morphological traits of spiders differ between ecological guilds: “Only few traits differed significantly between ecological guilds, ... it was not possible to unequivocally associate a set of morphometric traits with the relative ecological mode.” That study, however, lumped together all spiders with aerial webs and thus did not account for the evidence of important behavioral differences (e.g., attack behavior in orb webs compared with sheet webs) that might correlate with morphological differences. Analyses of morphology that avoid the temptations of extreme simplification may be more rewarding.

The great British naturalist William S. Bristowe (1939: viii) prefaced his *The Comity of Spiders* book with a challenging question: Why do nearly half of the species

and more than half of the population of British spiders belong to the family Linyphiidae? More than 80 years later we lack a clear answer to that question. The question itself would benefit from taking a more explicit comparative angle. Bristowe’s (1941: 503) closing chapter provides what he considered the most satisfactory answer to that question: climate (e.g., tolerance to low temperatures), an abundance of food supply (primarily collembolans and nematoceros flies), an ability to live in diverse habitats, and a partial immunity from predators (many linyphiids are distasteful to spiders and centipedes) would explain the abundance and diversity of linyphiids in the temperate regions. Bristowe’s hypotheses remain to be rigorously tested. Whether or not the linyphiid syndrome is responsible, at least in part, for the evolutionary diversification and ecological abundance of linyphiids is unknown. The fact that the families Pimoidae, Cyatholipidae, and Physoglenidae all appear to share several aspects of the linyphiid syndrome but nevertheless have relatively few species that are not as widespread or common suggests that this suite of traits is not the sole explanation for the evolutionary and ecological success of linyphiids.

Sticky Lines and Other Limitations of This Study

Contrary to previous conventional wisdom (e.g., Kaston, 1948; Bristowe, 1958; Comstock, 1967), the webs of many linyphiids contain substantial numbers of small sticky lines. They are difficult to perceive with the naked eye (Millidge, 1988; Peters and Kooor, 1991; Benjamin and Zschokke, 2002; Eberhard, 2021). In this study most webs were coated with powder to photograph them, so it was generally not possible to distinguish sticky from nonsticky lines. One exception was *Dubiaranea lugubris*, which had large, closely spaced droplets on lines in the sheet (Figs. 22C, D). Our only

other related observation was that the patches of “slime” on *Laminacauda magna* sheets (Fig. 40) were not sticky. The stickiness of the shiny, apparently slimy material covering of the naked sheets of *Tapinopa longidens* (Fig. 76A) was not tested. As already noted, fragmentary data indicate that there is probably substantial variation in the presence, the relative numbers, and the locations of sticky lines in linyphiid webs (Kullmann, 1971; Millidge, 1988; Peters and Kooor, 1991; Schütt, 1995; Benjamin and Zschokke, 2002; Eberhard, 2021). These variables thus constitute important added dimensions of linyphioid web diversity not covered in this study.

All of the photos in this study were made in the field, so the histories of webs were not known; some were probably freshly built, whereas others may have included lines added over a longer period of time. We may have overlooked webs like those of *Bathypantes eumenis* (Rybák, 2007) that were so sparse that we did not distinguish them from accumulations of drag lines.

Further Underexplored Aspects of Linyphioid Webs

Tensions on different lines are a largely unexplored aspect of web structure. It is possible, however, to intuit tensions indirectly from our photos. Suter (1984) showed that the “tensor” lines that produced dimples in the sheet of the bowl and doily spider *Frontinella pyramitela* increased the tensions on nearby lines in the sheet. The functional significance of this pattern of tensions is uncertain. It could simply be a guide to allow the spider to find a central resting site from which to monitor its web (Suter, 1984). In this species, the tension was greater in the “central area” of the cup-shaped sheet where the spider rested; the lines surrounding this area were less tense, whereas lines farther away, near attachments to the substrate, were more tense. We suppose that the dimples that we

documented here also produced local increases in tensions on sheet lines. Similar dimples occur in the sheets of several other spiders that have a more or less horizontal sheet suspended between tangles of lines, including diguetids, several theridiids, and the araneid *Cyrtophora citricola* (Eberhard, 2020).

Another aspect of linyphiid webs needing further exploration is the possibility that sheets sometimes function to accumulate pollen, fungal spores, or water droplets. Convincing demonstrations of pollen feeding are seen in *Frontinella pyramitela* and *Tennesseellum formicum* (Emerton, 1882): spiders used specialized behavior to feed on corn (*Zea mays* Linnaeus, 1753) pollen in their webs that did not simply involve incidental ingestion during web destruction (Peterson et al., 2010: 210). They fed relatively quickly (within about 30 minutes) after pollen was applied, apparently without breaking web lines “by drawing the pollen grains into their mouths with alternating cheliceral movements, chewing with the endites, and periodic expulsion and retrieval of a droplet of salivary liquid from the oral cavity.” On the other hand, *F. pyramitela* failed to derive nutrition from the abundant pollen of pine trees (Carrel et al., 2000).

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APPENDIX

Voucher specimens (unless otherwise mentioned, the voucher specimens will be deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZBASE Catalog Numbers are provided). The .NEF file name extensions correspond to original digital images; .TIF and TIFF correspond to digitized original slide film.

Cyatholipidae

Forstera sp., female. Australia Queensland, Atherton Tablelands, Land Rd., Rose Gums Wilderness Retreat ca. 13 km NE of Malanda, ridge trail behind Bowerbird Cabin, 17°18'50.6"S, 145°42'10.6"E, 725 m, 11.ii.2012, G. Hormiga (DSC_8144.NEF) (MCZ:IZ:164814).

Forstera sp., female. Australia Queensland, Atherton Tablelands, Land Rd., Rose Gums Wilderness Retreat ca. 13 km NE of Malanda, ridge trail behind Bowerbird Cabin, 17°18'50.6"S, 145°42'10.6"E, 725

m, 11.ii.2012, G. Hormiga (DSC_8129.NEF) (MCZ:IZ:164815).

Matilda sp., female. Western Australia, Two Road, Walpole-Nornalup National Park, 11.1 km 282° W Walpole, eucalypt forest and open heathland, night, 34°57'55.6"S, 116°36'23.8"E, ca. 40 m, 26.ii.2006, G. Hormiga (DSC_0218.NEF) (MCZ:IZ:164816).

Forstera sp., female. Australia, Queensland, Atherton Tablelands, Lake Tinaroo, Dambulla State Forest, dry forest, 17°10'30"S, 145°39'34"E, 810 m, 21.iv.2002, G. Hormiga (GH020421_R08_32_AUS.TIF, GH020421_R08_35_AUS.TIF, GH020421_R08_37_AUS.TIF) (MCZ:IZ:164817).

Forstera sp., female. Australia, New South Wales, Border Ranges National Park, Brindle Creek Rd., temperate rainforest, 28°22'42.2"S, 153°04'09.4"E, 713 m, 22.iii.2010, G. Hormiga (DSC_3143.NEF, DSC_3142.NEF) (MCZ:IZ:164818).

Teomenaarus sp., female, male. Australia, Queensland, Atherton Tablelands, Lake Tinaroo, Dambulla State Forest, dry forest, 17°10'30"S, 145°39'34"E, 810 m, 21.iv.2002, G. Hormiga (GH020421_R08_30_AUS.TIF) (MCZ:IZ:164819).

Teomenaarus sp., female, male. Australia, Queensland, Tamborine National Park, Witches Falls, rainforest, 27°56'27"S, 153°10'48"E, 17.iv.2002, G. Hormiga (GH020417_R04_23_AUS.TIF, GH020417_R04_19_AUS.TIF, GH020417_R04_24_AUS.TIF) (MCZ:IZ:164820).

Forstera sp., female. Australia New South Wales, Border Ranges National Park, Brindle Creek Rd. 28°22'42.2"S, 153°04'09.4"E, 713 m, temperate rainforest, 22.iii.2010, G. Hormiga (DSC_3132.NEF, DSC_3135.NEF) (MCZ:IZ:164821).

Teomenaarus sp., male, female. Australia, Queensland, Kuranda Environmental Park, 27.viii.1992, G. Hormiga (GH920827_R05_28_AUS.TIF, GH920827_R05_31_AUS.TIF, GH920827_R05_33_AUS.TIF) (MCZ:IZ:164822).

Forstera sp., female. Australia, Queensland, Atherton Tablelands, Rose Gums, rainforest, 17°18'44"S, 145°42'09"E, 750 m, 20.iv.2002, G. Hormiga (GH020420_R07_17_AUS.TIF) (MCZ:IZ:164823).

Forstera sp., female with spiderlings. Australia, Queensland, Atherton Tablelands, Lake Tinaroo, Dambulla State Forest, dry forest, 17°10'30"S, 145°39'34"E, 810 m, 21.iv.2002, G. Hormiga (GH020421_R08_18_AUS.TIF, GH020421_R08_17_AUS.TIF, GH020421_R08_20_AUS.TIF) (MCZ:IZ:164824).

Ulcembua sp., female. South Africa, Sodwana Bay National Park, Mgoboseleni trail, 27°32'34.9"S, 32°39'48.7"E, 50 m, 6.iv.2001, G. Hormiga (GH010406_R07_07_SAF.TIF, GH010406_R07_08_SAF.TIF, GH010406_R07_12_SAF.TIF) (MCZ:IZ:164825).

Wanzia fako, male. Cameroon, Fako Division, Mount Cameroon, north of Mapanja, mist forest on

south side, elev. 1,425 m, 4°06'28"N, 9°07'10"E, 27.i.1992, G. Hormiga (GH920126_R05_28_CAM.TIF) (MCZ:IZ:164826).

Wanzia fako, male, Cameroon, Fako Division, Mount Cameroon, north of Mapanja, mist forest on south side, elev. 1,425 m, 4°06'28"N, 9°07'10"E, 27.i.1992, G. Hormiga (GH920127_R06_07_CAM.TIF, GH920127_R06_27_CAM.TIF) (MCZ:IZ:164827).

Wanzia fako, female, male, Cameroon, Southwest Province, Fako Division, Mt. Cameroon, forest near Mann's Spring, elev. 2,050 m, 4°08'N, 9°07'E, 22.i.1992, G. Hormiga (GH920122_R04_07_CAM.TIF) (NMNH, Smithsonian Institution).

Wanzia fako, male, Cameroon, Southwest Province, Fako Division, Mt. Cameroon, forest near Mann's Spring, elev. 2,050 m, 4°08'N, 9°07'E, 24.i.1992, G. Hormiga (GH920124_R04_14_CAM.TIF, GH920124_R04_17_CAM.TIF, GH920124_R04_19_CAM.TIF) (MCZ:IZ:164829).

Physoglenidae

Chileotaxus sans, male, Chile, X Región de Los Lagos: Puyehue National Park, Sendero Anticura, 40°40'00"S, 72°10'30"W, 350 m, 30.xii.2000, G. Hormiga (GH000730_R03_37_CHI.tif, GH001230_R03_04_CHI.tif) (MCZ:IZ:164830).

Chileotaxus sans, Chile IX Región, Araucanía: Monumento Natural Contulmo, 38.01647916°S, 73.17933879°W, 355 m, 13.xi.2014, G. Hormiga (DSC_2028.NEF) (MCZ:IZ:164831).

Mangua medialis, male, New Zealand, South Island, WD, Fox Glacier, Westland Tai Poutini National Park, Glacier View Rd., Chalet Lookout Walk, 43°29'42.5"S, 170°01'54.8"E, 297 m, 2.ii.2012, G. Hormiga (DSC_7925.NEF) (MCZ:IZ:164832).

Pahora sp. New Zealand (CASENT9062577_CRW_0363_CEG) (CAS).

Physoglenes puyehue, female, Chile, X Región de Los Lagos: Puyehue National Park, Sendero Anticura, 40°40'0"S, 72°10'30"W, 350 m, 30.xii.2000, G. Hormiga (GH001230_R03_14_CHI.tif, GH001230_R03_18_CHI.tif) (MCZ:IZ:164833).

Tupua sp., female, Australia, Tasmania: Cradle Mountain-Lake St. Clair N. P., near Waldheim cabins, 22.6 km 202° SWS Moina, *Nothofagus* forest, 41°38'28.5"S, 145°56'26.5"E, 926 m, 3.iii.2006, G. Hormiga (DSC_0264.NEF) (MCZ:IZ:164834).

Paratupua sp., female, Australia, Victoria, nr. Warburton, O'Shannassy Aqueduct Trail, 37.74242°S, 145.71245°E, 302 m, 13.iv.2014, G. Hormiga (DSC_1392.NEF) (MCZ:IZ:164835).

Paratupua sp., male, Australia, Victoria, Acheron Way, NE of Warburton, mixed forest of Eucalyptus, *Nothofagus* and tree ferns, 37.68530°S, 145.72034°E, 766 m, 17.ii.2019, G. Hormiga (DSC_1532.NEF) (Univ. Barcelona, Facultat de Biologia).

Runga sp., juvenile, New Zealand, South Island, WD, Fox Glacier, Westland Tai Poutini National Park,

Glacier View Rd., Chalet Lookout Walk, 43°29'42.5"S, 170°01'54.8"E, 297 m, 2.ii.2012, G. Hormiga (DSC_7972.NEF) (MCZ:IZ:164836).

Runga sp., male, New Zealand, South Island, Slab Hut Creek campground, nr. Reefton, 42.15610701, 171.792631, 207 m, 16.i.2016, G. Hormiga (DSC_0064.NEF, DSC_0069.NEF) (MCZ:IZ:164837).

Runga sp., female, New Zealand, South Island: Victoria Forest Park, Tawhai Picnic Area, 42.14564597, 171.81514, 230 m, 17.i.2016, G. Hormiga (DSC_0071.NEF) (MCZ:IZ:164838).

Runga sp., female, New Zealand, South Island, Arthur's Pass National Park, Bridal Veil Track, 42°55'49.6"S, 171°33'43.4"E, 519 m, 4.ii.2012, G. Hormiga (DSC_7998.NEF) (MCZ:IZ:164839).

Pimoidae

Pimioa brevata Chamberlin & Ivie, 1943, female, USA, Oregon, Curry Co., Azalea State Park, 16.vii.1990, G. Hormiga (GH900716_R00_29_USA_Pimioa_brevata_ED.TIF) (NMNH, Smithsonian Institution).

Pimioa brevata, female, USA, Oregon, Humbug Mountain State Park, off Hwy. 101, trailhead to Humbug Mountain, 240 m, 19.viii.2008, G. Hormiga (DSC03994_ED) (MCZ:IZ:164841).

Pimioa cthulhu Hormiga, 1994, female, USA, California, Mendocino Co., Mendocino Woodland State Park, 39°20'04.9"N, 123°43'32.6"W, 280 m, 20.viii.2008, G. Hormiga (DSC03917_ED.jpg, DSC03992_ED.jpg, DSC_5047_ED.NEF, DSC_5057_ED.NEF) (MCZ:IZ:164842).

Linyphiidae

Acroterius GH02, juvenile, Taiwan, Pingtung Co., Li-Lung Mountain, N of Dungyuan Township, off County Rd. 199, 22.24056°N, 120.85497°E, 457 m, 29.vii.2013, G. Hormiga (T01) (DSC_0975.NEF, DSC_0959.NEF, DSC_0938.NEF) (MCZ:IZ:164843).

Acroterius GH01, male, Thailand, Chiang Mai Prov., Doi Inthanon N.P., cloud forest, Kew Mae Pan Nature trail, 18°33'19.9"N, 98°28'56.4"E, 2,170 m, 4.x.2003, G. Hormiga (GH031004_R03_21_THA_ED.TIF, GH031004_R03_22_THA_ED.TIF) (MCZ:IZ:164844).

Acroterius GH01, subadult female, Thailand, Chiang Mai Prov., Doi Inthanon N.P., cloud forest, Kew Mae Pan Nature trail, 18°33'19.9"N, 98°28'56.4"E, 2,170 m, 4.x.2003, G. Hormiga (GH031004_R03_25_THA_ED.TIF) (MCZ:IZ:164845).

Acroterius GH01, subadult female, Thailand, Chiang Mai Prov., Doi Inthanon N.P., cloud forest at summit, 18°35'21.4"N, 98°29'10.2"E, 2,590 m, 4.x.2003, G. Hormiga (GH031004_R03_29_THA_ED.TIF) (MCZ:IZ:164846).

Acroterius GH02, subadult male, Taiwan, Pingtung Co., Li-Lung Mountain, N of Dingnyan Township, off County Rd. 199, 22.24056°N, 120.85497°E, 457 m, 29.vii.2013, G. Hormiga (T01) (DSC_0964.NEF) (MCZ:IZ:164847).

Agyneta "CR01," female, Costa Rica, Heredia Prov., Puerto Viejo de Sarapiquí, Estación Biológica La Selva, 4.iv.1993, G. Hormiga (GH930404_R00_02_CRI_Meioneta.tif, GH930404_R00_07_CRI_Meioneta.tif) (NMNH, Smithsonian Institution).

Agyneta "CR01," female, Costa Rica, Heredia Prov., Puerto Viejo de Sarapiquí, Estación Biológica La Selva, 2.iv.1993, G. Hormiga (GH930402_R00_05_CRI.tif, GH930402_R00_10_CRI.tif) (MCZ:IZ:164849).

Agyneta micaria (Emerton, 1882), female, USA, Maryland, Prince George's Co., Patuxent Wildlife Research Center, 2.vi.1994, G. Hormiga (GH940602_R00_28_USA_Meioneta_sp2.tif, GH940602_R00_29_USA_Meioneta_sp2.tif) (MCZ:IZ:164850).

Agyneta nr. *luctuosa*, male, Guyana, 4.42 km S of Gunn's landing, Upper Takutu-Upper Essequibo, lowland blackwater rainforest, 1°36'46"N, W58°38'15", 240 m, 10.vii.1999, G. Hormiga (GH990710_04_01_RGUY_Meioneta.tif, GH990710_R04_05_GUY_Meioneta.tif, GH990710_R04_07_GUY_Meioneta.tif) (MCZ:IZ:164851).

Agyneta semipallida (Chamberlin & Ivie, 1944), female, USA, Maryland, Prince George's Co., Patuxent Wildlife Research Center, 19.v.1994, G. Hormiga (GH940519_R00_14_USA_Meioneta_sp7.tif, GH940519_R00_15_USA_Meioneta.tif) (MCZ:IZ:164852).

Agyneta sp. (undet.), female, USA, North Carolina, Macon Co., Glenn Falls, near Highlands, 35°01'N, 83°14'W, 22.vi.1991, G. Hormiga (GH910622_R00_17_USA_Meioneta.tif) (NMNH, Smithsonian Institution).

Agyneta sp., females, South Africa, Sodwana Bay National Park, Mgoboseleni trail, 27°32'34.9"S, 32°39'48.7"E, 50 m, 7.iv.2001, G. Hormiga (GH010407_R0S_02_SAF_Meioneta.tif, GH010407_R0S_04_SAF_Meioneta.tif) (MCZ:IZ:164853).

Agyneta sp. H101, female, USA, Hawaii, Oahu, Mt. Ka'ala, near access road to summit, 1,160 m, 13.viii.1995, G. Hormiga (GH950813_R04_01_HAW_Meioneta.tif) (NMNH, Smithsonian Institution).

Agyneta sp. H102, female, USA, Hawaii, Kauai, W of Wailua, 375–475 m, 16.viii.1995, G. Hormiga (GH950816_R06_15_HAW_Meioneta.tif, GH950816_R06_18_HAW_Meioneta.tif) (NMNH, Smithsonian Institution).

Agyneta sp., male (same species as above), South Africa, South Africa, St. Lucia Game Reserve, Fanies Island, 28°06'36.8"S, 32°25'52.5"E, 23–30 m, 4.IV.2001, 4.iv.2001, G. Hormiga (GH010404_R06_13_SAF_Meioneta.tif) (MCZ:IZ:164856).

Agyneta sp., male, Colombia, Valle del Cauca, P.N.N. Farallones de Cali, near Pance, Res. Nat. Hato Viejo, 3°20'53"N, 76°40'16.7"W, 2,300 m, 13.ii.1998, G. Hormiga (GH980213_R03_04_COL_Meioneta.tif) (MCZ:IZ:164857).

Agyneta sp., subadult male, Colombia, Valle del Cauca, P.N.N. Farallones de Cali, near Pance, Res. Nat. Hato Viejo, 3°20'53"N, 76°40'16.7"W, 2,300 m, 13.ii.1998, G. Hormiga (GH980213_R03_12_COL_Meioneta.tif, GH980213_R03_14_COL_Meioneta.tif) (MCZ:IZ:164858).

Australian genus 1 GH01, female, Australia, New South Wales, Dorrigo National Park, Dorrigo Rainforest Centre, along Wonga walk, 30°22'3.5"S, 152°43'42.4"E, 758 m, subtropical rainforest, 18.iii.2010, G. Hormiga (DSC_2776.NEF, DSC_2779.NEF, DSC_2780.NEF) (MCZ:IZ:164859).

Australian genus 1 GH01, female, Australia, New South Wales, Dorrigo National Park Dorrigo Rainforest Centre, along Wonga walk, subtropical rainforest, 30°22'3.5"S, 152°43'42.4"E, 758 m, 18.iii.2010, G. Hormiga (DSC_2794.NEF, DSC_2796.NEF, DSC_2801.NEF) (MCZ:IZ:164860).

Australian genus 1 GH01, female, Australia, Queensland, Lamington N.P., tracks near O'Reilly's, rain forest, 28°14'05"S, 153°08'13"E, 920 m, 14.iv.2002, G. Hormiga (GH020414_R01_08_AUS_Laetesia.tif) (MCZ:IZ:164861).

Australian genus 1 GH01, female, Australia, Queensland, Tamborine National Park, Witches Falls Rainforest, 27°56'27"S, 153°10'48"E, 17.iv.2002, G. Hormiga (GH020417_R04_31_AUS_Laetesia.tif, GH020417_R04_36_AUS_Laetesia.tif) (MCZ:IZ:164862).

Australian genus 1 GH01, male and female, Australia, Queensland, Lamington N.P., tracks near O'Reilly's, rain forest, 28°14'05"S, 153°08'13"E, 920 m, 18.vii.1992, G. Hormiga (GH920718_R01_05_AUS_Laetesia.tif, GH920718_R01_10_AUS_Laetesia.tif) (MCZ:IZ:164863).

Australian genus 1 GH02, female, Australia, Tasmania, Cradle Mountain National Park, near Waldheim cabins, 22.6 km 202° SWS Moina, *Nothofagus* forest, 41°38'28.5"S, 145°56'26.5"E, 926 m, 3.iii.2006, G. Hormiga (DSC_0268.NEF, DSC_0270.NEF) (MCZ:IZ:164864).

Australian genus 1 GH02, female, Australia, Tasmania, Franklin-Gordon Wild Rivers National Park, 26.4 km 157° SSE Queenstown, *Nothofagus* rainforest, 42°18'35.7"S, 145°36'56.9"E, 192 m, 10.iii.2006, G. Hormiga (DSC_0506.NEF, DSC_0511.NEF) (MCZ:IZ:164865).

Australian genus 1 GH03, female, Australia, Victoria, Dandenong National Park, Hardy Gully trail, *Eucalyptus regnans* and tree fern forest, 37.88829°S, 145.37200°E, 266 m, 18.iv.2014, G. Hormiga (DSC_1495.NEF, DSC_1497.NEF) (MCZ:IZ:164866).

Australian genus 1 GH03, female. Australia, Victoria, Dandenong National Park, Hardy Gully trail, *Eucalyptus regnans* and tree fern forest, 37.88529°S, 145.37200°E, 266 m, 18.iv.2014, G. Hormiga (DSC_1485.NEF) (MCZ:IZ:164867).

Australian genus 1 GH05, female. Australia, Tasmania, Mt. Field N.P., Tall Trees Trail, *Nothofagus*, *Eucalyptus regnans* and tree ferns rainforest, 42.68289°S, 146.70542°E, 259 m, 22.iv.2014, G. Hormiga (DSC_1592.NEF, DSC_1596.NEF) (MCZ:IZ:164868).

Australian genus 1 GH05, female. Australia, Tasmania, Weldborough Pass Scenic Reserve rainforest walk, 28.6 km, 280° WNW St. Helens, *Nothofagus* forest, 41°12'59.8"S, 147°56'18.2"E, 480 m, 6.iii.2006, G. Hormiga (DSC_0362.NEF) (MCZ:IZ:164869).

Australian genus 1 GH06, female. Australia, Tasmania, Mt. Field N.P., Tall Trees Trail, *Nothofagus*, *Eucalyptus regnans* and tree ferns rainforest, 42.68289°S, 146.70542°E, 259 m, 22.iv.2014, G. Hormiga (DSC_1585.NEF, DSC_1587.NEF) (MCZ:IZ:164870).

Australian genus 2 GH01, female. Australia, Queensland, Lamington N.P., tracks near O'Reilly's, rain forest, 28°14'05"S, 153°08'13"E, 920 m, 16.iv.2002, G. Hormiga (GH020416_R03_07_AUS.tif, GH020416_R03_09_AUS.tif) (MCZ:IZ:164871).

Australian genus 2 GH01, female. Australia, Queensland, Lamington N.P., tracks near O'Reilly's, rain forest, 28°14'05"S, 153°08'13"E, 920 m, 19.vii.1992, G. Hormiga (GH920719_R01_24_AUS.tif, GH920719_R01_26_AUS.tif) (NMNH, Smithsonian Institution).

Australian genus 3 GH01, female. Australia, New South Wales, Dorrigo National Park, Dorrigo Rainforest Centre, along Wonga walk, subtropical rainforest, 30°22'3.5"S, 152°43'42.4"E, 758 m, 19.iii.2010, G. Hormiga (DSC_2817.NEF, DSC_2819.NEF) (MCZ:IZ:164873).

Australian genus 3 GH01, female. Australia, Queensland, Lamington National Park, Bina Burra, rainforest, 28°12'11"S, 153°11'20"E, 910 m, 18.iv.2002, G. Hormiga (GH020418_R06_08_AUS_ED.tif) (MCZ:IZ:164874).

Australian genus 3 GH02, female. Australia, Queensland, Atherton Tablelands, Dambulla State Forest, Lake Tinaroo, dry forest, 17°10'30"S, 145°39'34"E, 810 m, 21.iv.2002, G. Hormiga (GH020421_R09_03_AUS.tif, GH020421_R09_05_AUS.tif) (MCZ:IZ:164875).

Australian genus 3 GH02, female. Australia, Queensland, Atherton Tablelands, Dambulla State Forest, Lake Tinaroo, dry forest, 17°10'30"S, 145°39'34"E, 810 m, 21.iv.2002, G. Hormiga (GH020421_R09_11_AUS.tif) (MCZ:IZ:164876).

Australian genus 4 GH01, female. Australia, Tasmania, Weldborough Pass Scenic Reserve rain-

forest walk, 28.6 km, 280° WNW St. Helens, *Nothofagus* forest, 41°12'59.8"S, 147°56'18.2"E, 480 m, 6.iii.2006, G. Hormiga (DSC_0339.NEF, DSC_0343.NEF) (MCZ:IZ:164877).

Australian genus 4 GH01, female. Australia, Tasmania, Weldborough Pass Scenic Reserve, rainforest walk, 28.6 km, 280° WNW St. Helens, *Nothofagus* forest, 41°12'59.8"S, 147°56'18.2"E, 480 m, 6.iii.2006, G. Hormiga (DSC_0348.NEF) (MCZ:IZ:164878).

Australolinyphia remota Wunderlich, 1976, subadult male. Australia, Queensland, Lamington N.P., tracks near O'Reilly's, rain forest, 28°14'05"S, 153°08'13"E, 920 m, 16.iv.2002, G. Hormiga (GH020416_R03_11_AUS_Austral_remot.tif, GH020416_R03_12_AUS_Austral_remot.tif) (MCZ:IZ:164879).

Australolinyphia remota Wunderlich, 1976, female. Australia, Queensland, Lamington N.P., tracks near O'Reilly's, rain forest, 28°14'05"S, 153°08'13"E, 920 m, 16.iv.2002, G. Hormiga (GH020416_R03_15_AUS_Austral_remot.tif, GH020416_R03_16_AUS_Austral_remot.tif) (MCZ:IZ:164880).

Bathyphantes pallidus, male. USA, Maryland, Prince George's Co., Patuxent Wildlife Research Center, 30.vi.1993, G. Hormiga (GH930630_R02_07_USA_Bathy_pallid.tif) (MCZ:IZ:164881).

Bathyphantes pallidus, subadult female. USA, Maryland, Prince George's Co., Patuxent Wildlife Research Center, 10.v.1994, G. Hormiga (GH940510_R00_21_USA_Bathy_pallid.tif, GH940510_R00_25_USA_Bathy_pallid.tif) (NMNH, Smithsonian Institution).

Diplothyron dianae, female. Costa Rica, Puntarenas Prov., Parque Internacional La Amistad (ACLA), Estación Pittier 009.01'N, 82.5°W, 1,890 m, 13.vi.1995, G. Hormiga (GH950613_R09_06_CRI_diplothy.tif, GH950615_R09_08_CRI_diplothy.tif) (MCZ:IZ:164883).

Diplothyron dianae, female. Costa Rica, Puntarenas Prov., Parque Internacional La Amistad (ACLA), Estación Pittier 009.01'N, 82.5°W, 1,675 m, 15.vi.1995, G. Hormiga (GH950615_R09_28_CRI_diplothy.tif, GH950615_R00_32_CRI_Diplothyron.tif) (MCZ:IZ:164884).

Diplothyron nubilosus Moreira & Hormiga, 2022, male and female. Panama, Prov. Chiriquí, Parque Internacional La Amistad, Las Nubes, ANAM, Sendero El Retoño, 8°53'37.8"N, 82°14'20.7"W, 18.vi.2008, G. Hormiga (DSC_4009.NEF, DSC_4010.NEF) (MCZ:IZ:164885).

Diplothyron nubilosus Moreira & Hormiga, 2022, female. Costa Rica, Cerro de la Muerte, near Albergue Cuericé, 9.533333°, -83.716389°, 2,505 m, 22.ii.1993, G. Hormiga (GH930222_R02_23_CRI_Dubiar_spec.tif, GH930222_R02_27_CRI_Dubiar_spec.tif) (NMNH, Smithsonian Institution).

Diplothyron nubilosus Morcira & Hormiga, 2022, female. Panama: Prov. Chiriquí, Parque Internacional La Amistad, Las Nubes, ANAM, Sendero El Retoño, 5°53'37.8"N, 82°14'20.7"W, 18.vi.2008, G. Hormiga (DSC_4011.NEF) (MCZ:IZ:164887).

Diplothyron nubilosus, male. Costa Rica, Cerro de la Muerte, near Albergue Cuericí, 9.533333°, -83.716389°, 2,505 m, 22.ii.1993, G. Hormiga (GH930222_R02_34_CRI_Dubiar_sp.tif) (NMNH, Smithsonian Institution).

Dubiaranca caledonica (Millidge, 1985), female. Chile: Bio Bio, Lago Lanalhue, ca. 5.2 km N of Contulmo, near cabin, 37°58'46.0"S, 73°14'46.6"W, 41 m, 13.xi.2014, G. Hormiga (DSC_1997.NEF, DSC_2000.NEF) (MCZ:IZ:164889).

Dubiaranca distincta (Nicolet, 1849), female. P.N. Puyehue, Anticura, 40°40'00"S, 72°10'30"W, 350 m, 2.i.2001, G. Hormiga (GH010102_R06_17_CHI_Dubiar_aysens.tif, GH010102_R06_19_CHI_Dubiar_aysens.tif) (MCZ:IZ:164890).

Dubiaranca distincta (Nicolet, 1849), female. P.N. Puyehue, below Antillanca, 40°46'30"S, 72°12'00"W, 1,000 m, 31.xii.2000, G. Hormiga (GH001231_R04_28_CHI_Dubiar_aysens.tif, GH001231_R04_25_CHI_Dubiar_aysens.tif) (MCZ:IZ:164891).

Dubiaranca distincta (Nicolet, 1849), male and subadult female. P.N. Puyehue, below Antillanca, 40°46'30"S, 72°12'00"W, 1,000 m, 29.xii.2000, G. Hormiga (GH001229_R01_17_CHI_Dubiar_aysens.tif) (MCZ:IZ:164892).

Dubiaranca fulgens Millidge, 1985, female. Chile, Reg. X (de Los Lagos), Osorno Prov., P.N. Puyehue, Los Mallines, bog, 40°46'0"S, 72°17'00"W, 700 m, 1.i.2001, G. Hormiga (GH010101_R05_19_CHI_Dubiar_fulg.tif, GH010101_R05_22_CHI_Dubiar_fulg.tif) (MCZ:IZ:164893).

Dubiaranca hospita (Keyserling, 1886), female. Trinidad and Tobago: Trinidad: Brasso Seco, trail off Madamas Rd. (TT11), 10.745566°, -61.25537803°, 185 m, 16.v.2017, G. Hormiga (DSC_0554.NEF, DSC_0544.NEF) (MCZ:IZ:164894).

Dubiaranca insulana Millidge, 1991, female. Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, area above the self-guided trail (JF07); -33.65377382°, -78.8431563°, 301 m, Luma (*Myrceugenia fernandeziana*) forest, 1.iv.2013, G. Hormiga (DSC_416.NEF, DSC_418.NEF, DSC_428.NEF) (MCZ:IZ:164895).

Dubiaranca lugubris Millidge, 1991, female. Colombia, P.N. Purace, Laguna San Rafael, 02°22'6.3"N, 76°20'47.9"W, 3,305 m, 15.ii.1998, G. Hormiga (GH980215_R04_01_COL_Dubiar_lug.tif, GH980215_R04_11_COL_Dubiar_lug.tif) (MCZ:IZ:164896).

Dubiaranca sp. DE1, female. Ecuador, Napo Prov., Sierra Azul, Hacienda Aragón, trail to Valle Hermoso, night, -0.6666667°, -77.9166667°, 2,300 m,

15.vi.1996, G. Hormiga (GH960615_R04_20_ECU_Dubiar_sp.tif, GH960615_R04_23_ECU_Dubiar_sp.tif) (MCZ:IZ:164897).

Dubiaranca sp. DE1, female. Ecuador, Napo Prov., Sierra Azul, Hacienda Aragón, -0.6666667°, -77.9166667°, 2,300 m, 10.vi.1996, G. Hormiga (GH960610_R01_04_ECU_Dubiar_sp.tif, GH960610_R01_08_ECU_Dubiar_sp.tif, GH960610_R01_09_ECU_Dubiar_sp.tif) (MCZ:IZ:164898).

Dubiaranca sp. DE2, female. Ecuador, Napo Prov., Sierra Azul, Hacienda Aragón, night, -0.6666667°, -77.9166667°, 2,300 m, 11.vi.1996, G. Hormiga (GH960611_R01_15_ECU_Dubiar_sp_ED.tif, GH960611_R01_11_ECU_Dubiar_sp_ED) (MCZ:IZ:164899).

Floronia bucculenta (Clerk, 1757), female. Sweden, Tullbotorp, nr. Ecology Lab Botaniska Inst., Biol. Station, 15.viii.1994, G. Hormiga (GH940813_R00_06_SWE_Floron_bucc.tif, GH940813_R00_09_SWE_Floron_bucc.tif) (MCZ:IZ:164900).

Frontinella pyramitela (Walckenaer, 1841), female. USA, Maryland, Prince George's Co., Patuxent Wildlife Research Center, 11.v.1994, G. Hormiga (GH940511_R02_30_USA_Frontin_pyram.tif, GH940511_R02_32_USA_Frontin_pyram.tif) (MCZ:IZ:164901).

Frontinella sp., female. Dominican Republic: Barahona Prov., Paraíso, Reserva Natural Cachote, cloud forest and secondary growth, 18°05'54.8"N, 71°11'22.0"W, 1,220 m, 6.iv.2005, G. Hormiga (GH050409_R02_20_DR_Frontinella_.jpg, GH050409_R02_28_DR_Frontinella_.jpg) (MCZ:IZ:164902).

Grammonota sp., juvenile. Costa Rica, Heredia Prov., Puerto Viejo de Sarapiquí, Estación Biológica La Selva, 3.iv.1993, G. Hormiga (GH930403_R06_15_CRI.tif) (NMNH, Smithsonian Institution).

Himalaphantes sp., female. Taiwan: Nantou Co., Beidongyianshan, nr. Renai Township, Highland Horticultural Experimental Station (T07), trail to Valle Hermoso, dense native forest, daytime-night, 24.07603°N, 121.13463°E, 1,965 m, 4.vii.2013, G. Hormiga (DSC_0991, DSC_0994) (MCZ:IZ:164904).

Himalaphantes sp., female. Taiwan: Nantou Co., Beidongyianshan, nr. Renai Township, Highland Horticultural Experimental Station (T07), dense native forest, daytime-night, 24.07603°N, 121.13463°E, 1,965 m, 4.vii.2013, G. Hormiga (DSC_0999, DSC_1005) (MCZ:IZ:164905).

Juanfernandezia melanocephala Millidge, 1991, female. Chile: Región V: Archipiélago de Juan Fernández, Isla Alejandro Selkirk, Quebrada Las Casas (Selkirk 04), -33.76586024°, -80.77361866°, 131 m, 12.iii.2015, G. Hormiga (DSC_2502.NEF, DSC_2500.NEF, DSC_2512.NEF) (MCZ:IZ:164906).

Juanfernandezia melanocephala Millidge, 1991, female. Chile: Región V: Archipiélago de Juan

Fernández, Isla Alejandro Selkirk, Las Chozas, patch of *Myrceugenia schulzei* trees (Selkirk 06), -33.75795409°, -80.77296722°, 613 m, 13.iii.2015, G. Hormiga (DSC_2542.NEF, DSC_2553.NEF) (MCZ:IZ:164907).

Juanfernandezia n. sp., female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Mirador de Selkirk, at lookout (JF03); -33.63685998°, -78.85140913°, 564 m, 25.iii.2013 G. Hormiga (DSC_0004, DSC_0011).

Juanfernandezia n. sp., female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, area above the self-guided trail (JF07); -33.65377382°, -78.8431563°, 301 m, Luma (*Myrceugenia fernandeziana*) forest, 1.iv.2013, G. Hormiga (DSC_0423.NEF, DSC_0430.NEF) (MCZ:IZ:164908).

Juanfernandezia n. sp., female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, self-guided trail (JF02); -33.6517568°, -78.84470687°, 338 m, Luma (*Myrceugenia fernandeziana*) forest, 24.iii.2013, G. Hormiga (DSC_0331.NEF) (MCZ:IZ:164909).

Labulla thoracica (Wider, 1834), Denmark, Eastern Jutland, Hestehaven, ca. 25 km NNE of Århus, mixed coastal forest, 56°17.46'N, 10°28.50'E, 29.viii-1.ix.1994, G. Hormiga (MCZ:IZ:164911).

Laetesia GH01, female, Australia, Queensland, Cape Tribulation National Park, Emmagen Creek, 26.vii.1992, G. Hormiga (GH920726_R05_02_AUS_Laetesia.tif, GH920726_R05_04_AUS_Laetesia_sp.tif, GH920726_R05_34_AUS_Laetesia_sp.tif) (NMNH, Smithsonian Institution).

Laetesia GH01, female, Australia, Queensland, Cape Tribulation National Park, Daintree N.P. Cape Tribulation, Jindalba Track, rainforest, 16°14'29"S, 145°25'59"E, 0 m, 25.iv.2002, G. Hormiga (GH020425_R12_02_AUS.TIF) (MCZ:IZ:164913).

Laetesia GH02, female, Australia, Queensland, Atherton Tablelands, Land Rd., Rose Gums Wilderness Retreat ca. 13 km NE of Malanda, ridge trail behind Bowerbird Cabin, 17°18'50.6"S, 145°42'10.6"E, 725 m, 8.ii.2012, G. Hormiga (DSC_8056.NEF, DSC_8051.NEF, DSC_8040.NEF, DSC_8045.NEF) (MCZ:IZ:164914).

Laetesia GH02, male, Australia, Queensland, Atherton Tablelands, Rose Gums, rainforest, 17°18'44"S, 145°42'09"E, 750 m, 20.iv.2002, G. Hormiga (GH020420_R07_03_AUS.tif, GH020420_R06_35_AUS.tif) (MCZ:IZ:164915).

Laetesia GH02, male, female, Australia, Queensland, Atherton Tablelands, Land Rd., Rose Gums Wilderness Retreat ca. 13 km NE of Malanda, ridge trail behind Bowerbird Cabin, 17°18'50.6"S, 145°42'10.6"E, 725 m, 8.ii.2012, G. Hormiga (DSC_8040.NEF, DSC_8045.NEF) (MCZ:IZ:164916).

Laetesia raveni Hormiga & Scharff, 2014, female, Australia, Queensland, Lamington N.P., Binna Burra,

rainforest, 28°12'11"S, 153°11'20"E, 910 m, 18.iv.2002, G. Hormiga (GH020418_R06_05_AUS.tif, GH020418_R06_07_AUS.tif, GH020418_R05_33_AUS.tif) (MCZ:IZ:164917).

Laetesia raveni Hormiga & Scharff, 2014, female, Australia, New South Wales, Dorrigo N.P., Dorrigo Rainforest Centre, along Wonga walk, subtropical rainforest, 30°22'3.5"S, 152°43'42.4"E, 758 m, 18-19.iii.2010, G. Hormiga (DSC_2834.NEF, DSC_2824.NEF, DSC_2828.NEF, DSC_2808.NEF, DSC_2804.NEF) (MCZ:IZ:164918).

Laetesia raveni Hormiga & Scharff, 2014, female, Australia, Victoria: Drummie Forest Walk, ca. 10 km E of Cann River, sifted litter, 37.56763°S, 149.27245°E, 144 m, 7-8.iv.2014, G. Hormiga (DSC_1325.NEF, DSC_1312.NEF) (MCZ:IZ:164919).

Laminacauda ansoni Millidge, 1991, female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, self-guided trail (JF02); 33.6517568°, -78.84470687°, 338 m, Luma (*Myrceugenia fernandeziana*) forest, 25.iii.2013, G. Hormiga (DSC_0035.NEF) (MCZ:IZ:164920).

Laminacauda ansoni Millidge, 1991, male, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, self-guided trail (JF02); -33.6517568°, -78.84470687°, 338 m, Luma (*Myrceugenia fernandeziana*) forest, 25.iii.2013, G. Hormiga (DSC_0020.NEF) (MCZ:IZ:164921).

Laminacauda ansoni, female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, area above the self-guided trail (JF07); -33.65377382°, -78.8431563°, 301 m, Luma (*Myrceugenia fernandeziana*) forest, 1.iv.2013, G. Hormiga (DSC_0043.NEF, DSC_0438.NEF) (MCZ:IZ:164922).

Laminacauda ansoni, male, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, self-guided trail (JF02); -33.6517568°, -78.84470687°, 338 m, Luma (*Myrceugenia fernandeziana*) forest, 25.iii.2013, G. Hormiga (DSC_0052.NEF) (MCZ:IZ:164923).

Laminacauda magna (no sex info), Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, self-guided trail (JF02); -33.6517568°, -78.84470687°, 338 m, Luma (*Myrceugenia fernandeziana*) forest, 25.iii.2013, G. Hormiga (DSC_0103.NEF, DSC_0105.NEF) (MCZ:IZ:164924).

Laminacauda magna Millidge, 1991, female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, self-guided trail (JF02); -33.6517568°, -78.84470687°, 338 m, 25.iii.2013, G. Hormiga (DSC_0018.NEF, DSC_0013.NEF) (MCZ:IZ:164925).

Laminacauda magna Millidge, 1991, female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, self-guided

trail (JF02): -33.6517568° , -78.84470687° , 338 m, Luma (*Myrceugenia fernandeziana*) forest, 25.iii.2013, G. Hormiga (DSC_0692.NEF, DSC_0694.NEF, DSC_0690.NEF, DSC_0697.NEF, DSC_0696.NEF) (MCZ:IZ:164926).

Laminacauda magna Millidge, 1991, female, Chile, Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, self-guided trail (JF02): -33.6517568° , -78.84470687° , 338 m, Luma (*Myrceugenia fernandeziana*) forest, 6.iv.2013, G. Hormiga (DSC_0674.NEF, DSC_0672.NEF, DSC_0678.NEF) (MCZ:IZ:164927).

Laminacauda magna, female, Chile, Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, self-guided trail (JF02): -33.6517568° , -78.84470687° , 338 m, Luma (*Myrceugenia fernandeziana*) forest, 6.iv.2013, G. Hormiga (DSC_0682.NEF, DSC_085.NEF, DSC_0680.NEF) (MCZ:IZ:164928).

Laminacauda magna, female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Mirador de Selkirk, after the lookout, W slope (JF04): -33.63708579° , -78.85237589° , 488 m, Luma (*Myrceugenia fernandeziana*) forest with tree ferns, 26.iii.2013, G. Hormiga (DSC_0093.NEF) (MCZ:IZ:164929).

Laminacauda malkini Millidge, 1991, female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Cerro Centinela trail, forest NE below ridge trail (JF10): -33.64479337° , -78.80540798° , 330 m, Luma (*Myrceugenia fernandeziana*) and Manzano (*Boehmeria excelsa*), no understory, secondary with ants and introduced spiders, 7.iv.2013, G. Hormiga (DSC_0709.NEF) (MCZ:IZ:164930).

Laminacauda malkini, female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Salsipuedes trail (JF09), native forest on slope at the end of the ridge trail, *Myrceugenia*, *Drymis*, and ferns, -33.62998749° , -78.84343307° , 408 m, 5.iv.2013, G. Hormiga (DSC_0584.NEF, DSC_0587) (MCZ:IZ:164931).

Laminacauda malkini, female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Cerro Centinela trail, forest NE below ridge trail (JF10): -33.64479337° , -78.80540798° , 330 m, 7.iv.2013, G. Hormiga (DSC_0712.NEF) (MCZ:IZ:164932).

Laminacauda malkini, subadult female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Salsipuedes trail (JF09), native forest on slope at the end of the ridge trail; *Myrceugenia*, *Drymis*, and ferns, -33.62998749° , -78.84343307° , 408 m, 5.iv.2013, G. Hormiga (DSC_0575.NEF, DSC_0578) (MCZ:IZ:164933).

Laminacauda parvipalpis Millidge, 1985, subadult male, female, Chile: V Región de Valparaíso: Los Manantiales, Zapallar, native coastal sclerophyll forest

with petras (*Myrceugenia*) (Los Mananti 02), -32.57103545° , -71.40048335° , 133 m, 7.iii.2015, G. Hormiga (DSC_2267.NEF) (MCZ:IZ:164934).

Laminacauda parvipalpis, female, Chile: V Región de Valparaíso: Los Manantiales, Zapallar, native coastal sclerophyll forest with petras (*Myrceugenia*) (Los Mananti 02), -32.57103545° , -71.40048335° , 133 m, 7.iii.2015, G. Hormiga (DSC_2307.NEF) (MCZ:IZ:164935).

Laminacauda parvipalpis, female, Chile: V Región de Valparaíso: Los Manantiales, Zapallar, native coastal sclerophyll forest with petras (*Myrceugenia*) (Los Mananti 02), -32.57103545° , -71.40048335° , 133 m, 7.iii.2015, G. Hormiga (DSC_2322.NEF) (MCZ:IZ:164936).

Laminacauda parvipalpis, juvenile (not certain it built this web), Chile: V Región de Valparaíso: Los Manantiales, Zapallar, native coastal sclerophyll forest with petras (*Myrceugenia*) (Los Mananti 02), -32.57103545° , -71.40048335° , 133 m, 7.iii.2015, G. Hormiga (DSC_2270.NEF) (MCZ:IZ:164937).

Laminacauda propinqua Millidge, 1991, female, Chile: Región V: Archipiélago de Juan Fernández, Isla Alejandro Selkirk, Quebrada Las Casas (Selkirk 04), -33.76586024° , -80.77361866° , 131 m, 12.iii.2015, G. Hormiga (DSC_2495.NEF, DSC_2519.NEF) (MCZ:IZ:164938).

Laminacauda propinqua Millidge, 1991, missing voucher, no sex info, Chile: Región V: Archipiélago de Juan Fernández, Isla Alejandro Selkirk, Quebrada Las Casas (Selkirk 04), -33.76586024° , -80.77361866° , 131 m, 12.iii.2015, G. Hormiga (DSC_2496.NEF) (MCZ:IZ:164939).

Laminacauda propinqua, female, Chile: Región V: Archipiélago de Juan Fernández, Isla Alejandro Selkirk, Las Chozas, *Myrceugenia schulzei* forest (Selkirk 05), -33.75734741° , -80.77097551° , 501 m, 13.iii.2015, G. Hormiga (DSC_2532.NEF, DSC_2537.NEF, DSC_2529.NEF) (MCZ:IZ:164940).

Laminacauda propinqua, male, Chile: Región V: Archipiélago de Juan Fernández, Isla Alejandro Selkirk, Las Chozas, *Myrceugenia schulzei* forest (Selkirk 05), -33.75734741° , -80.77097551° , 501 m, 13.iii.2015, G. Hormiga (DSC_2535.NEF) (MCZ:IZ:164941).

Laminacauda rubens Millidge, 1991, female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, self-guided trail (JF02): -33.6517568° , -78.84470687° , 338 m, Luma (*Myrceugenia fernandeziana*) forest, 25.iii.2013, G. Hormiga (DSC_0020.NEF, DSC_0026.NEF, DSC_0001.NEF) (MCZ:IZ:164942).

Laminacauda rubens Millidge, 1991, male, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, self-guided trail (JF02): -33.6517568° , -78.84470687° , 338 m, Luma (*Myrceugenia fernandeziana*) forest, 25.iii.2013,

G. Hormiga (DSC_0046.NEF, DSC_0318.NEF) (MCZ:IZ:164943).

Laminacauda sp. ("chpas"), subadult male, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, self-guided trail (JF02); -33.6517568°, -78.84470687°, 338 m, Luma (*Myrceugenia fernandeziana*) forest, 25.iii.2013, G. Hormiga (DSC_0304.NEF) (MCZ:IZ:164944).

Laminacauda sp. ("chdes"), male, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Plazoleta del Yunque, self-guided trail (JF02); -33.6517568°, -78.84470687°, 338 m, Luma (*Myrceugenia fernandeziana*) forest, 25.iii.2013, G. Hormiga (DSC_0299.NEF) (MCZ:IZ:164945).

Laminacauda sp. ("fch"), female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe Mirador de Selkirk, after the lookout, W slope (JF04); -33.63708579°, -78.85237589°, 488 m, Luma (*Myrceugenia fernandeziana*) forest with tree ferns, 26.iii.2013, G. Hormiga (DSC_0073.NEF, DSC_0077.NEF) (MCZ:IZ:164946).

Laminacauda sp. ("fPC"), female, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe Plazoleta del Yunque, area above the self-guided trail (JF07); -33.65377382°, -78.8431563°, 301 m, Luma (*Myrceugenia fernandeziana*) forest, 1.iv.2013, G. Hormiga (DSC_0409.NEF, DSC_0405.NEF, DSC_0413.NEF) (MCZ:IZ:164947).

Laminacauda sp., juvenile, Chile: V Región de Valparaíso: Los Manantiales, Zapallar, native coastal sclerophyll forest with petras (*Myrceugenia*) (Los Mananti 02); -32.57103545°, -71.40048335°, 133 m, 7.iii.2015, G. Hormiga (DSC_2264.NEF) (MCZ:IZ:164948).

Laminacauda tuberosa Millidge, 1991, Chile: Región V: Archipiélago de Juan Fernández, Isla Robinson Crusoe, Mirador de Selkirk, after the lookout, W slope (JF04); -33.63708579°, -78.85237589°, 488 m, Luma (*Myrceugenia fernandeziana*) forest with tree ferns, 26.iii.2013, G. Hormiga (DSC_0299.NEF) (MCZ:IZ:164949).

Laperousea blattifera (Urquhart, 1887), male, Australia: SE Queensland: Lamington N.P., road Canungra-O'Reilly's, dry forest, 28°08'25"S, 153°06'55"E, 750 m, 15-17.iv.2002, G. Hormiga (GH020417_R03_27_AUS_Laperousea.TIF, GH020417_R03_30_AUS_Laperousea.TIF) (MCZ:IZ:164950).

Laperousea sp. (GH01), female, Australia: Tasmania: Cradle Mountain-Lake St. Clair N.P., near Waldheim cabins, 22.6 km 202° SWS Moina, *Nothofagus* forest, 41°38'28.5"S, 145°56'26.5"E, 926 m, 3-5.iii.2006, G. Hormiga (DSC_0257.NEF, DSC_0256.NEF) (MCZ:IZ:164951).

Laperousea sp. (GH1677), female, Australia, Victoria: Drummer Forest Walk, ca. 10 km E of Cann River, sifted litter, 37.56763°S 149.27245°E, 144 m,

7.iv.2014, G. Hormiga (DSC_1292.NEF, DSC_1294.NEF) (MCZ:IZ:164952).

Lepthyphantes turbatrix (O. Pickard-Cambridge, 1877), male, USA, Virginia, Giles Co., Pembroke, Jefferson National Forest, Mountain Lake Biological Station, cabins area, 37.37712326°, -80.51833279°, 1130.387207 (Mtn Lk BS 01), 24.ix.2015, G. Hormiga (DSC_2520.NEF) (MCZ:IZ:164953).

Linyphia triangularis (Clerck, 1757), female, Sweden, Tullbotorp, nr. Ecology Lab Botaniska Inst., Biol. Station, 1.ix.1994, G. Hormiga (GH940815_R00_17_SWE_Linyph-triangul.TIF, GH940815_R00_20_SWE_Linyph-triangul.TIF, GH940815_R00_04_SWE_Linyph-triangul.TIF) (MCZ:IZ:164954).

Linyphia triangularis, female, Denmark, Eastern Jutland, Hestehaven, ca. 25 km NNE of Århus, mixed coastal forest, 56°17.46'N, 10°28.50'E, 1.ix.1994, G. Hormiga (GH940901_R00_20_DEN_Linyph-triangul.tif, GH940901_R00_21_DEN_Linyph-triangul.tif) (MCZ:IZ:164955).

Mecynidis sp., female, Cameroon, Fako Division, Mount Cameroon, north of Mapanja, mist forest on south side, elev. 1,425 m, 4°06'28"N, 9°07'10"E, 27.i.1992, G. Hormiga (GH920127_R05_25_CAM_Mecyn-sp.TIF, GH920127_R05_20_CAM_Mecyn-sp.TIF, GH920127_R05_26_CAM_Mecyn-sp.TIF, GH920127_R06_15_CAM_Mecyn-sp.TIF, GH920127_R06_16_CAM_Mecyn-sp.TIF) (NMNH, Smithsonian Institution).

Mermessus tridentatus (Emerton, 1882), female, USA, Maryland, Prince George's Co., Patuxent Wildlife Research Center, 19.iv.1994, G. Hormiga (GH940519_R02_07_USA_Eperig-trident.TIF) (MCZ:IZ:164957).

Microlinyphia dana (Chamberlin & Ivie, 1943), female, USA, Washington, Clallam Co., Olympic National Park, Elwha River, nr. Altaire Campground, 2.viii.1990, G. Hormiga (GH900802_R00_31_USA_Microliny-dana.tif) (NMNH, Smithsonian Institution).

Microlinyphia simoni van Helsdingen, 1970, female, Madagascar, Toamasina prov., Mitsinjo forest, Station Forstier Analamazaotra, 0.75 km N Andasibe; 18°56'51.4"S, 48°25'11"E, 906 m, 1.ii.2009, G. Hormiga (DSC_5990.TIF) (MCZ:IZ:164959).

Microlinyphia simoni, female, Madagascar, Fianarantsoa prov., P.N. Ranomafana, 1.68 km SW Ranomafana, 21°15'50.6"S, 47°25'09.6"E, 970 m, 12.i.2009, G. Hormiga (DSC_5921.TIF, DSC_5925.TIF, DSC_5449.TIF, DSC_5454.TIF) (MCZ:IZ:164960).

Neomaso patagonicus (Tullgren, 1901), female, Chile, Reg. X (de Los Lagos), Osorno Prov., P.N. Puyehue, above Antillanca, 40°46'30"S, 72°11'30"W, 1,050-1,350 m, 29.xii.2001, G. Hormiga (GH001229_R01_31_CHI_Neomaso.tif) (MCZ:IZ:164961).

Neomaso pollicatus (Tullgren, 1901), female, Chile, V Región de Valparaíso: Los Manantiales, Zapallar,

native coastal sclerophyll forest with petras (*Myrcogenia*), -32.57103545° , -71.40048335° , 133 m, 7.iii.2015, G. Hormiga (DSC_2280.NEF, DSC_229S.NEF, DSC_2309.NEF) (MCZ:IZ:164962).

Neomaso sp., subadult female, Chile, Reg. X (de Los Lagos), Osorno Prov., P.N. Puyehue, above Antillanca, $40^{\circ}46'30''\text{S}$, $72^{\circ}11'30''\text{W}$, 1,050–1,350 m, 29.xii.2001, G. Hormiga (GH001229_R01_31_CHI_Neomaso.tif) (MCZ:IZ:164963).

Neriere albolimbata (Karsch, 1879), subadult female, Taiwan, Hsinchu Co., nr. Jianshi Township, off Rd. 60 (T11), 24.67244°N , $121.27955^{\circ}\text{E}$, 1,385 m, native forest (oak, Lauraceae), 8.vii.2013, G. Hormiga (DSC_105S.NEF, DSC_1059.NEF) (MCZ:IZ:164964).

Neriere albolimbata, female, Taiwan, Hsinchu Co., nr. Jianshi Township, off Rd. 60 (T11), 24.67244°N , $121.27955^{\circ}\text{E}$, 1,385 m, native forest (oak, Lauraceae), 8.vii.2013, G. Hormiga (DSC_105S.NEF, DSC_1093.NEF, DSC_1050.NEF) (MCZ:IZ:164965).

Neriere clathrata (Sundevall, 1830), female, USA, Maryland, Prince George's Co., Patuxent Wildlife Research Center, 19.vii.1993, G. Hormiga (GH930701_R00_24_USA_Neriere_clathr.TIF, GH930701_R00_26_USA_Neriere_clathr.TIF, GH930701_R00_29_USA_Neriere_clathr.TIF, GH930701_R00_34_USA_Neriere_clathr.TIF, GH930701_R00_32_USA_Neriere_clathr.TIF, GH930701_R00_33_USA_Neriere_clathr.TIF) (MCZ:IZ:164966).

Neriere clathrata, female, USA, Maryland, Prince George's Co., Patuxent Wildlife Research Center, 10.v.1994, G. Hormiga (GH940510_R00_29_USA_Neriere_clathr.TIF, GH940510_R00_30_USA_Neriere_clathr.TIF, GH940510_R00_34_USA_Neriere_clathr.TIF) (MCZ:IZ:164967).

Neriere digna (Keyserling, 1886), female, USA, Oregon, Lane Co., Siuslaw National Forest, 14.vii.1990, G. Hormiga (GH900714_R00_21_USA_Neriere_digna.TIF, GH900714_R00_1S_USA_Neriere_digna.TIF) (NMNH, Smithsonian Institution).

Neriere helsdingeni (Locket, 1968), female, Cameroon, Southwest Prov., Fako Div., Limbe subdiv., 1.4 km NE of Etome, 04.05°N , 09.125°E , 400 m, 16.i.1992, G. Hormiga (GH920116_R02_20_CAM_Neriere_helsd.TIF, GH920116_R02_21_CAM_Neriere_helsd.TIF) (MCZ:IZ:164969).

Neriere helsdingeni, female, Cameroon, Southwest Province, Fako Division, Mt. Cameroon, forest near Mann's Spring, elev. 2,050 m, $4^{\circ}08'\text{N}$, $9^{\circ}07'\text{E}$, 23.i.1992, G. Hormiga (GH920123_R03_2S_CAM_Neriere_helsd.TIF, GH920123_R03_1_CAM_Neriere_helsd.TIF, GH920123_R03_33_CAM_Neriere_helsd.TIF) (NMNH, Smithsonian Institution).

Neriere helsdingeni, female, Cameroon, Southwest Province, Fako Division, Mt. Cameroon, forest near Mann's Spring, elev. 2,050 m, $4^{\circ}08'\text{N}$, $9^{\circ}07'\text{E}$, 23.i.1992, G. Hormiga (GH920125_R04_22_CAM_Neriere_helsd.TIF, GH920125_R04_23_CAM_Neriere_helsd.TIF, GH920125_R04_22_CAM_Neriere_helsd.TIF, GH920125_R04_25_CAM_Neriere_helsd.TIF) (MCZ:IZ:164971).

Neriere litigiosa (Keyserling, 1886), female, USA, California, Grizzly Creek Redwoods State Park, 18.vii.1990, G. Hormiga (GH900718_R00_18_USA_Neriere_litig.TIF) (NMNH, Smithsonian Institution).

Neriere oxycera Tu & Li, 2006, male and female, Thailand, Chiang Mai Prov., Doi Chiang Dao WS, Amphien Chiangdao, below guest house along road, $19^{\circ}19'13.2''\text{N}$, $98^{\circ}49'47.0''\text{E}$, ca. 1,500 m, 2.X.2003, G. Hormiga (GH031002_R01_14_THA_.TIF) (MCZ:IZ:164973).

Neriere litigiosa (Keyserling, 1886), females, USA, Washington, USA, Washington, Whatcom Co., 4 km W of Lynden, $48^{\circ}56'48''\text{N}$, $122^{\circ}27'25''\text{W}$, August 2018, W.G. Eberhard (MCZ:IZ:164974).

Neriere oxycera, female, Thailand, Chiang Mai Prov., Doi Chiang Dao WS, Amphien Chiangdao, below guest house along road, $19^{\circ}19'13.2''\text{N}$; $98^{\circ}49'47.0''\text{E}$, ca. 1,500 m, 2.X.2003, G. Hormiga (GH031002_R01_22_THA_.TIF, GH031002_R01_24_THA_.TIF, GH031002_R01_28_THA_.TIF, GH031002_R01_31_THA_.TIF) (MCZ:IZ:164975).

Neriere sp. GH01 (GH1401), male and female, Taiwan, Hsinchu Co., nr. Jianshi Township, off Rd. 60 (T11), 24.67244°N , $121.27955^{\circ}\text{E}$, 1,385 m, native forest (oak, Lauraceae), 8.vii.2013, G. Hormiga (DSC_1100.NEF) (MCZ:IZ:164976).

Neriere sp. GH02 (GH1397), female, Taiwan, Hsinchu Co., nr. Jianshi Township, off Rd. 60 (T11), 24.67244°N , $121.27955^{\circ}\text{E}$, 1,385 m, native forest (oak, Lauraceae), 8.vii.2013, G. Hormiga (DSC_1108.NEF, DSC_1104.NEF) (MCZ:IZ:164977).

Neriere sp. GH03 (GH1398), female, Taiwan, Hsinchu Co., nr. Jianshi Township, off Rd. 60 (T11), 24.67244°N , $121.27955^{\circ}\text{E}$, 1,385 m, native forest (oak, Lauraceae), 8.vii.2013, G. Hormiga (DSC_1076.NEF, DSC_1077.NEF, DSC_1081.NEF) (MCZ:IZ:164978).

Neriere sp. GH03 (GH1398), male and female, Taiwan, Hsinchu Co., nr. Jianshi Township, off Rd. 60 (T11), 24.67244°N , $121.27955^{\circ}\text{E}$, 1,385 m, native forest (oak, Lauraceae), 8.vii.2013, G. Hormiga (DSC_1043.NEF, DSC_1036.NEF) (MCZ:IZ:164979).

Neriere variabilis (Banks, 1892), female, USA, Maryland, Prince George's Co., Patuxent Wildlife Research Center, 1.vii.1993, G. Hormiga (GH930701_R00_12_USA_Neriere_variab.TIF, GH930701_R00_13_USA_Neriere_variab.TIF) (MCZ:IZ:164980).

Neriere variabilis, female, USA, Maryland, Prince George's Co., Patuxent Wildlife Research Center, 29.vi.1993, G. Hormiga (GH930629_R00_29_USA_Neriere_variab.TIF, GH930629_R00_33_USA_Neriere_variab.TIF) (MCZ:IZ:164981).

New genus MPME sp. 1, female, Costa Rica, Cerro de la Muerte, near Albergue Cuercici, 9.533333° , -83.716389° , 2,505 m, 21.ii.1993, G.

Hormiga (GH930221_R02_17_CRI_Dubiar_sp.tif, GH930221_R02_10_CRI_Dubiar_sp.tif) (MCZ:IZ:164982).

Notholepthyphantes australis (Tullgren, 1901), female. Chile, Reg. X (de Los Lagos), Osorno Prov., P.N. Puyehue, 40°46'30"S, 72°12'00"W, 700 m, 31.xii.2000, forest with *Nothofagus* and *Chusquea*, G. Hormiga (GH001231_R04_21_CHI_Nothelep_austr.TIF, GH001231_R04_19_CHI_Nothelep_austr.TIF) (MCZ:IZ:164983).

Notholepthyphantes australis, female. Chile, Reg. X (de Los Lagos), Osorno Prov., P.N. Puyehue, Anticura, 40°40'00"S, 72°10'30"W, 350 m, 2.i.2001, forest, G. Hormiga (GH010102_R06_12_CHI_Nothelep_austr.TIF, GH010102_R06_13_CHI_Nothelep_austr.TIF) (MCZ:IZ:164984).

Novafrofrontina sp., female. Brazil, Roraima, Municipalidade Caracará, Arquipélago de Mariuí e Baixo Rio Branco, Médio Rio Negro Rio Jufarí, Caicubí, trail leading east of Caicubí community, -1.028499501°, -62.08976808°, 71 m, 29.v.2012, G. Hormiga (DSC_9313.NEF, DSC_9318.NEF) (MCZ:IZ:164985).

Novafrofrontina sp., female. Brazil, Roraima, Municipalidade Caracará, Arquipélago de Mariuí e Baixo Rio Branco, Médio Rio Negro Rio Jufarí, Caicubí, trail leading east of Caicubí community, -1.029293519°, -62.09583163°, 34 m, 30.v.2012, G. Hormiga (DSC_9407.NEF, DSC_9413.NEF) (MCZ:IZ:164986).

Novafrofrontina sp., female. Brazil, Roraima, Municipalidade Caracará, Arquipélago de Mariuí e Baixo Rio Branco, Médio Rio Negro Rio Jufarí, Comunidade Caicubí, Pupunha, -0.988992071°, -62.0973496°, 38 m, 28.v.2012, G. Hormiga (DSC_9231.NEF, DSC_9233.NEF) (MCZ:IZ:164987).

Novafrofrontina uncata (F. O. Pickard-Cambridge, 1902), female. Costa Rica, Heredia Prov., Puerto Viejo de Sarapiquí, Estación Biológica La Selva, 6.iv.1993, G. Hormiga (GH930406_R08_34_CRI_Novafro_uncata.tif, GH930406_R08_35_CRI_Novafro_uncata.tif) (NMNH, Smithsonian Institution).

Novafrofrontina uncata, female. Costa Rica, Sirena, Parque Nacional Corcovado, 3.iii.1993, G. Hormiga (GH930303_R00_01_CRI_Novafro_uncata.tif, GH930303_R00_15_CRI_Novafro_uncata.tif, GH930303_R00_29_CRI_Novafro_uncata.tif, GH930303_R00_23_CRI_Novafro_uncata.tif) (MCZ:IZ:164989).

Novafrofrontina uncata, subadult female. Costa Rica, Heredia Prov., Puerto Viejo de Sarapiquí, Estación Biológica La Selva, 6.iv.1993 (GH930406_R08_26_CRI_Novafro_uncata.tif, GH930406_R08_31_CRI_Novafro_uncata.tif) (MCZ:IZ:164990).

Orsonwelles ambersonorum Hormiga, 2002, female. Hawaii, Oahu, Ko'olau Range, Mount Tantalus, 21°19'58.9"N, 157°48'58.3"W, ca. 530 m, 11.viii.1995, G. Hormiga (Orsonwelles ambersonorum_F_ow31plates_E.tif) (NMNH, Smithsonian Institution).

Orsonwelles calx Hormiga, 2002, subadult female. Hawaii, Kauai, Laau Ridge, NNW of Puu Kamaha, 22°08'13.1"N, 159°32'22.9"W, 4.v.2000, ca. 1,225 m, G. Hormiga (Orsonwelles calx_F_ow32plates_E.tif) (MCZ:IZ:164992).

Orsonwelles falstaffius Hormiga, 2002, female. Hawaii, East Maui, Haleakala, Waikamoi Preserve, ca. 1,860 m, 21.viii.1995, G. Hormiga (Orsonwelles falstaffius_F_ow35plates_E.tif) (MCZ:IZ:164993).

Orsonwelles falstaffius Hormiga, 2002, juvenile, detail of repair work in main platform. Hawaii, East Maui, Haleakala, Waikamoi Preserve, ca. 1,860 m, 21.viii.1995, G. Hormiga (Orsonwelles falstaffius_J_ow35plates_E.tif, Orsonwelles falstaffius_J_ow37plates_E.tif) (MCZ:IZ:164994).

Orsonwelles falstaffius Hormiga, 2002, subadult female. Hawaii, East Maui, Haleakala, Waikamoi Preserve, ca. 1,860 m, 21.viii.1995, G. Hormiga (Orsonwelles falstaffius_sF_ow36plates_E.tif) (NMNH, Smithsonian Institution).

Orsonwelles graphicus (Simon, 1900), female. Hawaii, Hawaii, Kahaula Natural Area Reserve, 19°26'43.0"N, 155°07'20.5"W, ca. 680 m, 24.iv.1999, G. Hormiga (Orsonwelles graphicus_F_ow40plates.tif) (MCZ:IZ:164996).

Orsonwelles graphicus, female. Hawaii, Hawaii, Pu'u MaKa'aala Natural Area Reserve, off Stainback Hwy., 19°33'54.6"N, 155°13'53.7"W, ca. 680 m, 27.iv.1999, G. Hormiga (Orsonwelles graphicus_F_ow41plates.tif, Orsonwelles graphicus_F_ow42plates.tif, Orsonwelles graphicus_F_ow43plates.tif) (MCZ:IZ:164997).

Orsonwelles macbeth Hormiga, 2002, female. Hawaii, Molokai, Kamakou Preserve, Peopae trail, 21°07'16.4"N, 156°53'46.8"W, 1,265 m, 12.v.2000, G. Hormiga (Orsonwelles macbeth_F_ow23plates.tif) (MCZ:IZ:164998).

Orsonwelles macbeth, female. Hawaii, Molokai, Kamakou Preserve, Pu'u KoleKole Cabin, 21°06'27.2"N, 156°53'49.2"W, ca. 1,165 m, 14.v.2000, G. Hormiga (Orsonwelles macbeth_F_ow24plates.tif, Orsonwelles macbeth_F_ow25plates.tif) (MCZ:IZ:164999).

Orsonwelles malus Hormiga, 2002, female. Hawaii, Kauai, Near Waialae State Cabin, 22°04'56.9"N, 159°35'9.7"W, ca. 1,045 m, 9.v.2000, G. Hormiga (Orsonwelles malus_F_ow20plates.tif) (MCZ:IZ:165000).

Orsonwelles malus, female. Hawaii, Kauai, Kokee State Park, Nualolo trail, 22°07'59.2"N, 159°39'40.0"W, ca. 1,060 m, 16.viii.1995, G. Hormiga (Orsonwelles malus_F_ow22plates.tif) (MCZ:IZ:165001).

Orsonwelles malus, juvenile. Hawaii, Kauai, Kokee State Park, Nualolo trail, 22°07'59.2"N, 159°39'40.0"W, ca. 1,060 m, 15.viii.1995, G. Hormiga (Orsonwelles malus_J_ow21plates.tif) (NMNH, Smithsonian Institution).

Orsonwelles othello Hormiga, 2002, female. Hawaii, Molokai, Kamakou Preserve, intersect. Maunahui Rd./Puu Kauwa Rd., 545 m, 25.viii.1995, G. Hormiga (Orsonwelles_othello_F_ow34plates.tif, Orsonwelles_othello_F_ow33plates.tif) (NMNH, Smithsonian Institution).

Orsonwelles polites Hormiga, 2002, juvenile. Hawaii, Oahu, Waianae Mts., Honouliuli For. Res., off road to Palikea, 21°24'33.1"N, 158°05'55.1"W, 17.v.2000, G. Hormiga (Orsonwelles_polites_J_ow27plates.tif) (MCZ:IZ:165004).

Orsonwelles polites, female. Hawaii, Oahu, Waianae Mts., Palikea, 21°23'26.6"N, 158°05'55.6"W, ca. 780 m, 9.iv.1999, G. Hormiga (Orsonwelles_polites_F_ow30plates.tif) (MCZ:IZ:165005).

Orsonwelles polites, female. Hawaii, Oahu, Mt. Kaala, near access road to summit, ca. 515 m, 13.viii.1995, G. Hormiga (Orsonwelles_polites_F_ow29plates.tif, Orsonwelles_polites_F_ow28plates.tif) (NMNH, Smithsonian Institution).

Orsonwelles polites, female. Hawaii, Oahu, Waianae Mts.: Waianae Kai Natural Area Reserve, 21°29'24.3"N, 158°09'26.8"W, ca. 530–680 m, 7.iv.1999, G. Hormiga (Orsonwelles_polites_F_ow26plates.tif) (MCZ:IZ:165007).

Ostearius melanopygius (O. Pickard-Cambridge, 1880), female. Hawaii, Oahu, Waianae Mts., Palikea, 21°23'26.6"N, 158°05'55.6"W, 9.iv.1999, ca. 780 m, G. Hormiga (GH990409_R04_05_USA_Ostear_melano.tif) (MCZ:IZ:165008).

Pityohyphantes costatus (Hentz, 1850), juvenile. USA, Virginia, Giles Co., Pembroke, Jefferson National Forest, Mountain Lake Biological Station, cabins area, 37.37712326°, -80.51833279°, 1,130.387207, 24.ix.2015, G. Hormiga (DSC_2798.NEF, DSC_2802.NEF, DSC_2796.NEF) (MCZ:IZ:165009).

Pityohyphantes costatus, female. USA, Maryland, Prince George's Co., Patuxent Wildlife Research Center, 10.v.1994, G. Hormiga (GH940510_R00_02_USA_Pityohy_cost.TIF, GH940510_R00_09_USA_Pityohy_cost.TIF, GH940510_R00_04_USA_Pityohy_cost.TIF) (MCZ:IZ:165010).

Pityohyphantes costatus, subadult male. USA, Virginia, Giles Co., Pembroke, Jefferson National Forest, Mountain Lake Biological Station, cabins area, 37.37712326°, -80.51833279°, 1,130.387207, 24.ix.2015, G. Hormiga (DSC_2807.NEF, DSC_2814.NEF) (MCZ:IZ:165011).

Pocobletus sp. GH01, female. Panama, Prov. Panamá: P. Nac. Altos de Campana, 8°41'00.4"N, 79°55'47.4"W, 895 m, 19.vi.2007, G. Hormiga (DSC_2835_ED.NEF) (MCZ:IZ:165012).

Pocobletus sp. exoGH03, female. Colombia, Departamento Valle del Cauca, near Cali, Finca La Zingara, nr. km 18, 3°32'22.6"N, 76°36'19.4"W, 1,900 m, 11.ii.1995, G. Hormiga (GH980211_R00_19_

COL_Execchop_sp3_ED.tif, GH980211_R00_21_COL_Execchop_sp3_ED.tif) (MCZ:IZ:165013).

Pocobletus sp. exoGH05, female. Colombia, Cundinamarca, Silvania, ca. 15 km from Sibaté, Recebera Agua Bonita, Cerro de San Miguel, Vereda El Provenir, 4°25.88'N, 74°19.422'W, 2,440–2,560 m, 1.ii.1998, G. Hormiga (GH980201_R00_09_COL_Execchop_sp5_ED.tif) (MCZ:IZ:165014).

Pocobletus sp. exoGH01, juvenile. Costa Rica, Puntarenas Prov., Parque Internacional La Amistad (ACLA), Estación Pittier 009.01'N, 82.5'W, 1,890 m, 12.vi.1995, G. Hormiga (GH950612_R00_14_CRI_Exocora_sp1_ED.tif, GH950612_R00_15_CRI_Exocora_sp1_ED.tif) (MCZ:IZ:165015).

Pocobletus sp. exoGH02, female. Costa Rica, Puntarenas Prov., Parque Internacional La Amistad (ACLA), Estación Pittier 009.01'N, 82.5'W, 1,890 m, 12.vi.1995, G. Hormiga (GH950612_R00_17_CRI_Exocora_sp2_ED.tif, GH950612_R00_22_CRI_Exocora_sp2_ED.tif) (MCZ:IZ:165016).

Pocobletus sp. exoGH02, female. Costa Rica, Puntarenas Prov., Parque Internacional La Amistad (ACLA), Estación Pittier 009.01'N, 82.5'W, 1,890 m, 13.vi.1995, G. Hormiga (GH950613_R00_30_CRI_Exocora_sp2_ED.tif, GH950613_R00_32_CRI_Exocora_sp2_ED.tif) (MCZ:IZ:165017).

Pocobletus sp. GH01, female. Panama: Prov. Panamá: P. Nac. Altos de Campana, 8°41'00.4"N, 79°55'47.4"W, 895 m, 18.vi.2007, G. Hormiga (DSC_2693_ED.NEF, DSC_2695_ED.NEF) (MCZ:IZ:165018).

Pocobletus sp. GH01, female. Panama: Prov. Panamá: P. Nac. Altos de Campana, 8°41'00.4"N, 79°55'47.4"W, 895 m, 19.vi.2007, G. Hormiga (DSC_2848_ED.NEF) (MCZ:IZ:165019).

Pocobletus sp. GH03, subadult female. Ecuador, Napo Prov., Sierra Azul, Hacienda Aragón, -0.6666667°, -77.9166667°, 2,300 m, 14.vi.1996, G. Hormiga (GH960614_R00_25_ECU_Pocoblet_sp3_ED.tif) (MCZ:IZ:165020).

Pocobletus sp. GH03, female. Ecuador, Napo Prov., Sierra Azul, Hacienda Aragón, -0.6666667°, -77.9166667°, 2,300 m, 12.vi.1996, G. Hormiga (GH960612_R01_27_ECU_Pocoblet_sp3ED.tif, GH960612_R01_32_ECU_Pocoblet_sp3ED.tif) (MCZ:IZ:165021).

Pocobletus sp. GH03, male. Ecuador, Napo Prov., Sierra Azul, Hacienda Aragón, -0.6666667°, -77.9166667°, 2,300 m, 14.vi.1996, G. Hormiga (GH960614_R02_18_ECU_Pocoblet_sp3_ED.tif) (MCZ:IZ:165022).

Pocobletus sp. GH10, female. Ecuador, Prov. Napo, Parque Nacional Yasuni, Reserva Étnica Huaorani, Estación Biológica Onkone Gare, lowland rain forest, 0°39'10"S, 76°26'0"W, 220 m, 21.vi.1996, G. Hormiga (GH960621_R07_25_ECU_Pocoblet_sp10_ED.TIF) (MCZ:IZ:165023).

Pocobletus sp. GH10, female. Ecuador, Prov. Napo, Parque Nacional Yasuni, Reserva Étnica Huaorani, Estación Biológica Onkone Gare, lowland rain forest, 0°39'10"S, 76°26'0"W, 220 m, 20.vi.1996, G. Hormiga (GH960620_R07_13_ECU_Pocoblet_sp10_ED.TIF, GH960620_R07_16_ECU_Pocoblet_sp10_ED.TIF) (MCZ:IZ:165024).

Pocobletus sp. GH11, female. Guyana, 4.42 km S of Gunn's landing, Upper Takutu–Upper Essequibo, lowland blackwater rainforest, 1°36'46"N, 58°38'15"W, 240 m, 16.vii.1999, G. Hormiga (GH990716_R07_26_GUY_Pocoblet_sp11_ED.TIF, GH990716_R07_31_GUY_Pocoblet_sp11_ED.TIF) (MCZ:IZ:165025).

Pocobletus sp. GH11, female. Guyana, 4.42 km S of Gunn's landing, Upper Takutu–Upper Essequibo, lowland blackwater rainforest, 1°36'46"N, 58°38'15"W, 240 m, 6.vii.1999, G. Hormiga (GH990706_R03_22_GUY_Pocoblet_sp11_ED.TIF) (MCZ:IZ:165026).

Pocobletus sp. GH11, female. Guyana, 4.42 km S of Gunn's landing, Upper Takutu–Upper Essequibo, lowland blackwater rainforest, 1°36'46"N, 58°38'15"W, 240 m, 6.vii.1999, G. Hormiga (GH990706_R03_20_GUY_Pocoblet_sp11_ED.TIF) (MCZ:IZ:165027).

Pocobletus sp. GH11, female. Guyana, 4.42 km S of Gunn's landing, Upper Takutu–Upper Essequibo, lowland blackwater rainforest, 1°36'46"N, 58°38'15"W, 240 m, 17.vii.1999, G. Hormiga (GH990717_R08_03_GUY_Pocoblet_sp11_ED.tif) (MCZ:IZ:165028).

Pocobletus sp. GH28, female. Argentina, P. Nac. Iguazu, area Cataratas, 13.xii.1999, M. J. Ramírez (MR990713_X01_09_ARG_Pocoblet_sp28_ED.jpg). (MACN).

Pocobletus sp. GH28, Argentina, P. Nac. Iguazu, 6 km E seccional Yacuy, 16.xii.1999, M. J. Ramírez (MR990716_X00_03_ARG_Pocoblet_sp28_ED.jpg). (MACN).

Pocobletus sp. GH28, female. Argentina, P. Nac. P. Nac. Iguazu, RN 101, 6 km E seccional Yacuy, 16.xii.1999, M. J. Ramírez (MR990716_X16_36_ARG_Pocoblet_sp28_ED.jpg). (MACN).

Pocobletus sp. GH28, female. Argentina, P. Nac. Iguazu, RN 101, 6 km E seccional Yacuy, 16.xii.1999, M. J. Ramírez (MR990716_X00_01_ARG_Pocoblet_sp28_ED.jpg). (MACN).

Pocobletus sp. GH31, juvenile. Panama, Prov. Chiriquí, Parque Internacional La Amistad, Las Nubes, ANAM, 8°53'37.8"N, 82°14'20.7"W, 18.vi.2008, G. Hormiga (DSC_4015_ED.NEF, DSC_4023_ED.NEF) (MCZ:IZ:165029).

Pocobletus sp. GH32, female. Brazil, Roraima, Municipalidade Caracaraí, Arquipélago de Mariuí e Baixo Rio Branco, Médio Rio Negro Rio Jufarí, Caicubí, trail leading east of Caicubí community, -1.028499501°, -62.08976808°, 71 m, 29.V.2012, G.

Hormiga (DSC_9278.NEF, DSC_9280.NEF) (MCZ:IZ:165030).

Pocobletus sp. GH32, subadult male. Brazil, Roraima, Municipalidade Caracaraí, Arquipélago de Mariuí e Baixo Rio Branco, Médio Rio Negro Rio Jufarí, Caicubí, trail leading east of Caicubí community, -1.028499501°, -62.08976808°, 71 m, 29.V.2012, G. Hormiga (DSC_9240.NEF, DSC_9237.NEF) (MCZ:IZ:165031).

Pocobletus sp. GH32, subadult male. Brazil, Roraima, Municipalidade Caracaraí, Arquipélago de Mariuí e Baixo Rio Branco, Médio Rio Negro Rio Jufarí, Caicubí, trail leading east of Caicubí community, -1.028499501°, -62.08976808°, 71 m, 29.V.2012, G. Hormiga (DSC_9287.NEF, DSC_9285.NEF) (MCZ:IZ:165032).

Pocobletus sp. GH32, male. Brazil, Roraima, Municipalidade Caracaraí, Arquipélago de Mariuí e Baixo Rio Branco, Médio Rio Negro Rio Jufarí, Caicubí, trail leading east of Caicubí community, -1.028499501°, -62.08976808°, 71 m, 29.V.2012, G. Hormiga (DSC_9294.NEF, DSC_9295.NEF) (MCZ:IZ:165033).

Pocobletus sp. GH33, female. Dominican Republic, Sierra de Bahoruco, Reserva Cachote (GH050407_R01_03_DR_Pocobletus_ED.jpg, GH050407_R01_05_DR_Pocobletus_ED.jpg) (MCZ:IZ:165034).

Pocobletus sp. GH33, male. Dominican Republic: Barahona Prov., Paraíso, Reserva Natural Cachote, cloud forest and secondary growth, 18°05'54.8"N, 71°11'22.0"W, 1,220 m, 8.iv.2005, G. Hormiga (GH050408_R01_36_DR_Pocobletus_ED.jpg) (MCZ:IZ:165035).

Pocobletus sp. GH33, female. Dominican Republic: Barahona Prov., Paraíso, Reserva Natural Cachote, cloud forest and secondary growth, 18°05'54.8"N, 71°11'22.0"W, 1,220 m, 9.iv.2005, G. Hormiga (GH050409_R02_36_DR_Pocobletus_ED.jpg) (MCZ:IZ:165036).

Pocobletus sp. GH33, female. Dominican Republic: Barahona Prov., Paraíso, Reserva Natural Cachote, cloud forest and secondary growth, 18°05'54.8"N, 71°11'22.0"W, 1,220 m, 9.iv.2005, G. Hormiga (GH050409_R03_01_DR_Pocobletus_ED.jpg, GH050409_R03_07_DR_Pocobletus_ED.jpg) (MCZ:IZ:165037).

Pocobletus sp. GH33, subadult male. Dominican Republic: Barahona Prov., Paraíso, Reserva Natural Cachote, cloud forest and secondary growth, 18°05'54.8"N, 71°11'22.0"W, 1,220 m, 8.iv.2005, G. Hormiga (GH050408_R02_06_DR_Pocobletus_ED.jpg, GH050408_R02_12_DR_Pocobletus_ED.jpg) (MCZ:IZ:165038).

Pocobletus versicolor (Millidge, 1991), female. Costa Rica, Heredia Prov., Puerto Viejo de Sarapiquí, Estación Biológica La Selva, 5.iv.1993, G. Hormiga (GH930405_R08_11_CRI_Execop_versic_ED.TIF,

GH930405_R08_14_CRI_Execchop_versic_ED.TIF) (MCZ:IZ:165039).

Pocobletus versicolor (Millidge, 1991), male. Ecuador, Prov. Napo, Parque Nacional Yasuni, Reserva Étnica Huaorani, Estación Biológica Onkone Gare, lowland rain forest, 0°39'10"S, 76°26'0"W, 220 m, 21.vi.1996, G. Hormiga (GH960621_R07_20_ECU_Execchop_versic_ED.TIF, GH960621_R07_21_ECU_Execchop_versic_ED.TIF) (MCZ:IZ:165040).

Pocobletus versicolor (Millidge, 1991), juvenile. Costa Rica, Heredia Prov., Puerto Viejo de Sarapiquí, Estación Biológica La Selva, 3.iv.1993, G. Hormiga (GH930403_R06_01_CRI_Execchop_versic_ED.tif, GH930403_R06_07_CRI_Execchop_versic_ED.tif) (MCZ:IZ:165041).

Putaoa seediq Hormiga & Dimitrov, 2017, subadult female. Taiwan, Nantou Co., Huisun Forestry Station, Xiaochu Mtn., 12.98 km NNE Puli, roadcut in forest, 24.07693°N, 121.03348°E, 1,095 m, 5.vii.2013, G. Hormiga (DSC_1012_ED.NEF, DSC_1014_ED.NEF) (MCZ:IZ:165042).

Putaoa seediq, juvenile. Taiwan, Nantou Co., Huisun Forestry Station, Xiaochu Mtn., 12.98 km NNE Puli, roadcut in forest, 24.07693°N, 121.03348°E, 1,095 m, 5.vii.2013, G. Hormiga (DSC_1030_ED.NEF, DSC_1031_ED.NEF) (MCZ:IZ:165043).

Putaoa seediq, juvenile. Taiwan, Nantou Co., Huisun Forestry Station, Xiaochu Mtn., 12.98 km NNE Puli, roadcut in forest, 24.07693°N, 121.03348°E, 1,095 m, 5.vii.2013, G. Hormiga (DSC_1022_ED.NEF, DSC_1025_ED.NEF) (MCZ:IZ:165044).

Sphecozone bicolor (Nicolet, 1849), female. Chile, Región de La Araucanía: Huerquehue National Park, Sendero Ñirrico, -39.16400202°S, -71.71957796°W, 778 m, 23.xi.2019, G. Hormiga (DSC_2621_ED.NEF, DSC_2600_ED.NEF) (MCZ:IZ:165045).

Sphecozone bicolor (Nicolet, 1849), 1985, juvenile. Chile, Reg. X (de Los Lagos), Osorno Prov., P.N. Puyehue, above Antillanca, 40°46'30"S, 72°11'30"W, 1,300 m, 30.xii.2000, G. Hormiga (GH001230_R02_27_CHI_Sphecozone_ED.TIF, GH001230_R02_30_CHI_Sphecozone_ED.TIF) (MCZ:IZ:165046).

Tapinopa bilineata Banks, 1893, juvenile. USA, Maryland, Prince George's Co., Patuxent Wildlife Research Center, 21.vi.1994, G. Hormiga (GH940621_R00_27_USA_Tapinopa_ED.TIF, GH940621_R00_23_USA_Tapinopa_ED, GH940621_R00_24_USA_Tapinopa_ED) (MCZ:IZ:165047).

Tapinopa longidens (Wider, 1834), female. Sweden, Tullbotorp, nr. Ecology Lab Botaniska Inst., Biol. Station, 15.viii.1994, G. Hormiga (GH940815_R00_14_SWE_Tapin_longi.tif) (MCZ:IZ:165048).

Tapinopa vara Locket, 1982, female. Thailand, Naratiwat Prov., Waeng District, Hala Bala WS,

Research Station, 5°47'44.8"N, 101°50'4.2"W, 190–200 m, 13.x.2003, G. Hormiga, Bala (GH031013_R06_05_THA_ED.TIF, GH031013_R06_03_THA_ED.TIF) (MCZ:IZ:165049).

Tenuiphantes flavipes (Blackwall, 1854), female. Denmark, Eastern Jutland, Hestehaven, ca. 25 km NNE of Århus, mixed coastal forest, 56°17.46'N, 10°28.50'E, 1.ix.1994, G. Hormiga (GH940901_R00_11_DEN_Tenuiph_flav_ED.TIF, GH940901_R00_33_DEN_Tenuiph_flav_ED.TIF, GH940901_R00_12_DEN_Tenuiph_flav_ED.TIF) (MCZ:IZ:165050).

Walckenaeria? sp., female. Costa Rica, Puntarenas Prov., Parque Internacional La Amistad (ACLA), Estación Pittier 009.01'N: 82.5°W, 1,890 m, 13.vi.1995, G. Hormiga (GH950613_R00_36_CRI_Walcken_ED.TIF, GH950613_R00_37_CRI_Walcken_ED.TIF) (MCZ:IZ:165051).

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Photo on the front cover:

The web of an undescribed species of linyphiid genus *Acroterius* from Taiwan. Photo by Gustavo Hormiga.

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